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A. G. TANSLEY

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## THE BIOTIC COMMUNITY

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*(Read August 19th, 1930. International Botanical Congress, Cambridge.)*

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## I. INTRODUCTORY REMARKS.

In stating that specialisation, despite the obvious blessings it has bestowed, nevertheless is in some senses a hindrance to the progress of knowledge, I admit that I am uttering a truism. But are not truisms sometimes—through their very self-evidence—overlooked! With reference to our own great subject, I fear that over-specialisation is spelling a narrower and ever less co-ordinated concept of ecology. To many botanists ecology is but plant ecology, while I realise that some of my friends in the field of zoology take an equally parochial view<sup>1</sup>. We are becoming more and more inclined to work in non-co-ordinated departments—for example, to-day I am addressing an official meeting of plant

<sup>1</sup> Although Prof. V. E. Shelford (38, p. 235) holds that while animal ecologists have been forced to notice plants, many plant ecologists have entirely ignored animals.

ecologists, not a meeting of *ecologists*! Of all scientific workers perhaps the last who can afford to work in isolation is the ecologist.

I am to speak to you upon a subject around which the cross-currents of controversy have begun to swirl, and around which increasingly tempestuous seas are destined to rage. That subject is the grand one of *biotic communities*—with special reference to the place of animals in our concepts of the organisation and structure of communities.

As one who first entered the sphere of plant ecology, but who soon found that animals could not be relegated to a minor rôle in the study of community structure and functions, I humbly invite your attention to this important matter, for earnest and early attention it requires. It is scarcely necessary to remind you that one of the fundamental problems—fundamental because, in the absence of a clear-working solution, so much that depends upon it cannot be organised and directed adequately—is that pertaining to the organisation and structure of communities. A logical working concept of the community is essential to the development of the science of ecology.

## II. OBJECTS.

My desire is to review broadly the attitudes of ecologists toward the place of animals in natural communities, to describe a few of my own experiences in the study of this fascinating subject, to ask your especial consideration of the biotic community concept, and to solicit your criticism.

## III. A RÉSUMÉ OF VIEWS REGARDING THE RELATIONS OF PLANTS AND ANIMALS IN NATURAL COMMUNITIES.

Disregarding purely passing references, there is not a very large body of literature referring to the philosophical and scientific principles regarding the relations of plants and animals in natural communities.

If the view (5) that the essence of ecology lies in thinking of the environment in physical terms be neglected, we naturally arrive at the following classification of concepts:

(1) Animals are biotic factors external to the plant community—the view point of most plant ecologists.

(2) There are animal communities to which the plants are a portion of the habitat—the attitude of many animal ecologists.

(3) Plants and animals are inter-related, co-acting constituents of an integrated biotic community.

Let us briefly consider these concepts:

### (1) ANIMALS AS BIOTIC FACTORS EXTERNAL TO THE PLANT COMMUNITY.

Literature subscribing to this view is scattered and voluminous; this is the best supported concept so far as plant-ecologists are concerned. We can consider several of the more important references only:

Warming (52, p. 82), referring to non-living factors and plant competition, holds that animal life—he cites insects, earthworms and other small animals—has a profound influence upon the nature and the economy of vegetation. With that width of vision for which his writings are notable, Warming (52, p. 77) stresses that between the plant life and the animal life of any place there exists a reciprocal relation intimate as well as complex. His references (52, p. 366) to a community of living beings with lives interwoven into a common existence, almost inclines me to doubt whether Warming really was a staunch supporter of the view that animals act as factors external to the plant community.

Flahault and Schröter (21, p. 24), as reporters to the Commission on Phytogeographical Nomenclature, include animals (soil fauna, pollinators, dispersers, enemies) as biological factors of the habitat.

Tansley (41, p. 118; 42, pp. 166–8; 43, p. 680; 44, pp. 140–50) agrees that philosophically there is something to be said for the conception that plants and animals together form a sociological unit. On this argument, however, he considers that to complete the picture the inorganic factors of the habitat should be included in the concept of the community—and these, he says, obviously cannot be considered as *members* of the community, though they are certainly integral parts of the “system” of which the community is the conspicuous expression. It is as logical, he concludes, to take the biotic factors as external as to take the inorganic, and in practice it is necessary to study as a separate biotic factor any collection of animals which may have marked effect upon the plants.

A broad and interesting treatment is given by Yapp (57, pp. 10–11) who asks whether we should include in the same communities higher plants, lower plants, and animals. Holding that if the limits of plant communities and animal communities be proved to coincide to any appreciable extent, we might have to revise our concept of the plant community, Yapp summarises the then prevailing—and according to him *crude*—concept as that of a community of mainly higher plants living together in a habitat modified by other organisms—that is by biotic factors. Further, he thinks that we possibly may consider the plant communities and the animal communities in any given habitat as woven into “a complex but unstable web of life. The character of the web may change...during...succession...but the web itself remains.”

The valuable work of Farrow (20) and Watt (53, 54) as regards animals influencing British vegetation is based upon the view-point that the animals act as external factors.

Osborn (28), in a recent paper on the biological factor in the study of Australian vegetation, looks upon human agency (e.g. exploitation, firing of vegetation, introduction of exotic plants and animals) as a biotic factor of the habitat.

(2) ANIMAL COMMUNITIES TO WHICH THE PLANTS ARE A PORTION OF  
THE HABITAT.

Even as the majority of plant ecologists lean to animals being external to plant communities, so do the majority of the much smaller band of animal ecologists believe that plants should be considered as portion of the habitat, and not as members of the community.

We find that Brooker Klugh (26, p. 367) in his attempt to classify all biota ecologically, upon the basis of habitat, thinks that from the standpoint of animal life, plants are part of the habitat. Pearce (29, p. 279) is of the same view: plants afford protection and food to animals.

In his excellent book Chapman (7, p. 149) considers the animal alone as a constituent of the community, plants being included in biotic factors of the environment. In this connection it is not without interest to remind you that his classification of "animals active" for those organisms causing changes in their environment (7, p. 178) is the correlative of Tansley's (43, p. 680) "*auto-genic* succession," a plant succession brought about by the reaction of the plants themselves, and the equivalent of Tansley's "*allogenic* succession" produced by external biotic factors, for example the progressive action of animals.

Elton, in his suggestive book (19), treats animal communities as entities which are basically related to plants by food chains: plants may act as limiting factors to animals either in connection with food or with breeding or both. He does suggest the working out first of the stages of the plant succession, and then endeavouring to correlate with such stages the animal communities.

Adams (1, p. 13) considers plants as part of the environment of animal communities.

(3) PLANTS AND ANIMALS AS INTER-RELATED, CO-ACTING CONSTITUENTS  
OF AN INTEGRATED BIOTIC COMMUNITY.

In a very general manner Möbius (27), in his researches into the ecology of the oyster, seems to have been a pioneer in the concept that plants and animals together may form a biotic community—his *Biocönose* or *Lebens-gemeinschaft*—in possession of certain definite territory.

No development of the concept appears to have taken place until 1905, when Clements suggested identity between many plant communities and animal communities. In 1916 Clements (9) advanced the concept of the *biome*, or biotic community constituted by plants and animals. Owing to the large number of passing references in the literature by Clements and his chief associates—V. E. Shelford, W. P. Taylor, Vorhies, Bird and Shackelford—no attempt is made to deal in detail with these; the papers are cited in the references to literature (8, 9, 10, 11, 12, 13, 14, 15, 16, 36, 37, 38, 39, 45, 46, 47, 48, 49, 50).



For sake of emphasising the importance of considering plants and animals together as mutually interacting members of a community, the concept of the biotic community is put forward. As the seral and climax stages in vegetation are looked upon as the groundwork in which animals find their proper setting, such a concept is held as indispensable to the study of the causes and development of communities. The consideration of plant communities and animal communities as separate entities does violence to the facts presented in Nature, and what is more, acts adversely in that it obscures the fundamental relation between plants and animals. All along, however, it is conceded that as plants, in addition to giving physiognomy to the biotic community, control the animals by means of food, cover, shelter, provision of breeding sites, the functions of the plant matrix will necessarily very largely rule.

Clements and Shelford (14) have prepared an as yet unpublished scheme for the nomenclature and classification of biotic communities. In this scheme—which I have been able to see through the courtesy of my friend Dr Clements—it is definitely stated that the *biome* or plant-animal community is the basic unit, that is, there are not two separate communities, plant and animal, in the same area. As regards the nomenclature of biotic communities, it is of interest to note that Prof. V. E. Shelford (38), in his paper "Some Concepts of Bio-ecology" (which I have seen in manuscript, through the kindness of the author), writes: "The often mentioned effect of the bison on grassland is a matter in point, for if the bison held some of the mixed prairie in a short grass stage, then short grass is the bio-ecological climax, and its proper bio-ecological designation is *Stipa-Bison*."

It is of importance to note that as early as 1913, that is, three years before Clements (9) definitely advanced the concept of the *biome*, Vestal (51) suggested the concept of "single biotic associations." His grounds were that plant and animal associations were co-extensive, and to a large degree interdependent. Shelford (35, p. 20) two years later wrote that it seemed that the causes of plant and animal succession went hand in hand, as agreement between animal communities and plant communities was evidently the rule.

In his study of the animal ecology of an Illinois elm-maple forest, Weese (55) urges that the division into animal communities and plant communities is often an entirely arbitrary one.

The dominants of a given community may be either plants or animals or partially plants and partially animals.

Blake (6), comparing the animal communities of coniferous and deciduous forests, adopts the bio-ecological classification of Shelford and Towler (39).

That Cooper (17) believes that "plants and animals together constitute our communities," and that the distinction between pure plant and pure animal communities is an artificial one, is noteworthy.

Jones (25, p. 504) insists that in an ecological classification, plants and animals should be included in the same communities.

In his account of the distribution of animals in a Tropical South American rain forest, Allee (2, p. 466) considers the biota as a unit. He concludes that, in the tropical forest, the inter-relations of plants and animals are more vital than the inter-relations among animals. By the following year Allee (3, p. 439) went so far as to conclude that there are *rarely* plant and animal communities—the sole realities are the biotic communities, groups of plants and animals integrated into a community.

Having touched upon the views of other workers, it is incumbent to proceed to a short account of some of my own experiences in the study of natural communities.

#### IV. THE STUDY OF THE INTER-RELATIONS OF PLANTS AND ANIMALS IN NATURAL COMMUNITIES: CERTAIN EXPERIENCES.

We are to consider two such diverse regions as the humid temperate sub-tropical forests of the Knysna, Cape Province, South Africa, and the vast seasonally semi-arid steppes of the Great East African Plateau.

##### (1) STUDIES IN THE KNYSNA FORESTS.

These are relatively extensive, evergreen temperate sub-tropical forests lying along the coastal plateaux in the districts of George-Knysna-Humansdorp. They are luxuriant, dense, and possessed of a climax flora of upwards of sixty species of trees and large woody shrubs. Important forest trees are *Podocarpus* spp., *Olea laurifolia*, *Ocotea bullata*, *Apodytes dimidiata*, *Platylophus* and *Cunonia*.

During five years' intimate association with the seral and climax stages of these forests, I irresistibly had my attention drawn to the profound rôle played in their life-history by animals great and small. I attempt to summarise the nature of such inter-relations as seem especially worthy of note.

##### (a) *Biotic inter-relations in experimental screens.*

Some suggestive information relating to biotic inter-relations was yielded by a series of experiments really carried out with the prime object of studying the influences upon forest soils of varying degrees of insolation (31, 32).

Forest soil from the same site under high canopy in undisturbed condition to 2.5 to 3 ft., was placed in four large restio-thatch screens—the roofs and sides of which were readily penetrable by rain—and submitted for 2½ years to light intensities of 0.5, 0.2, 0.06 and 0.01 of full sunlight respectively, and to related differences in other important physical factors. Equal-aged, equal-conditioned seedlings of the same species (the principal forest trees *Ocotea bullata* E. Mey., *Cunonia capensis* L., *Platylophus trifolius* Don, *Apodytes dimidiata* E. Mey., *Curtisia faginea* Ait., *Olea laurifolia* Lam., *Podocarpus elongata* L'Herit., *P. Thunbergii* Hook.) were grown under the four sets of conditions. No watering and no weeding were done after the first few weeks.

The major edaphic factors, along with the prime aerial factors, were kept under measurement. At the end of  $2\frac{1}{2}$  years there had been some decided changes in aerial factors in the screens showing marked development of fast-growing sedges, herbs and shrubs, while the edaphic factors had changed to a striking degree. These changes have been published in detail (32) but may be summarised thus: The soil in the screens which experienced 0.5 and 0.2 light intensity had decreased appreciably in physical and chemical quality, particularly in permeability and air capacity; moisture content had been reduced, while poorly decomposed organic matter had increased; the pH values had decreased; solutes had been much diminished by the rampant weeds. The soil in the 0.06 light intensity had appreciably improved in permeability and air capacity; its pH had increased, its moisture content had been conserved, while the solutes readily available to plants had risen. In the lowest light intensity—0.01—the soil had not altered much, except that the pH had been lowered in the presence of increased, not fully decomposed organic matter; the total soluble salts had decreased slightly.

In the cultures experiencing light intensities of 0.5 and 0.2, dense "weed" vegetation appeared within several months, but no appreciable "weed growth" developed under the intensity of 0.06 until nearly 2 years after, and then was confined to open communities of *Pteridium aquilinum* and *Pteris dentata*; no weeds established themselves under the intensity of 0.01.

On account of the dense weed communities (chiefly *Helichrysum petiolatum*, *H. parviflorum*, *Berzelia*, *Ursinea*, and Cyperaceae) under the light intensities of 0.5 and 0.2, some of the seedling trees in these cultures received less light (e.g. 0.005 to 0.009 in the first culture, 0.002 to 0.0009 in the second, at 3 to 6 in. above the ground) than those in the cultures under the intensity of 0.01. An important feature is that the weed communities drew upon much of the moisture from the upper 6 to 9 in. of the soil.

Thermometric observations revealed that at times the weed communities acted as thermal blankets, higher temperatures being recorded under them than above. At such times the saturation deficit was usually greater under the weeds than above, while the evaporating power of the air due to the decreased rate of wind movement was considerably less under the weeds than above.

The general development and height increment of the tree seedlings and weed communities were kept under observation. In the instances of the tree seedlings the comparative root and stem length, number and area of leaves, fresh, dry and ash weights of selected average plants were determined quantitatively from time to time; the mean width and the nature of the tissues of the leaves of such average plants were measured by means of microscopic sections.

The seedlings in the cultures experiencing 0.5 and 0.2 light intensities and covered in the dense weed growth were non-thrifty in every sense, those under the intensity 0.01 were moribund, those under intensity 0.06 were the finest in the series. The seedlings in general vigour and rate of increment reflected

## The Biotic Community

a suggestive manner the nature of the habitat complexes provided, screen screen.

At this stage emerge the points I wish to bring to your particular attention:

In the provision of particular aerial conditions to the uniform natured soil, and in allowing all vegetation that would establish, to develop absolutely controlled, I consider that I produced, under experimental controlled conditions, the several stages of a forest secondary succession. At all events, quadrat studies in fired and felled portions of the natural forests satisfy me that I am correct in making this assumption. So far as the present theme is concerned, I am especially anxious to make clear the fact that, while there were most interesting and instructive reciprocal reactions as to physical conditions and vegetation, there were in addition just as striking features exhibited by the animal population. This is of no passing interest only, for the fact that apart from certain wide-ranging, stable forms, the animal species and numbers change with or just after the changes in vegetation stages, is singularly ordered with meaning for the ecologist. It brings home to him the complex inter-relation of the organisms within a natural habitat.

I regret that I have opportunity only of summarising the principal phenomena relating to the animals within the screens. For sake of brevity we may consider the communities under light intensities 0.5 and 0.2 together; we treat separately the communities under intensities 0.06 and 0.01.

The original mean number of Acanthodrilidae per square yard to the depth of 12 in., was between eight and nine. By the end of 2½ years the communities under 0.5 and 0.2 light intensity showed between three and four to the square yard, the community under 0.06 showed between eleven and twelve, and that under 0.01 intensity between four and five. This interesting feature is referred to again when we come to consider the conditions in the forests themselves.

The spectacular snail *Achatina zebra* and smaller native snails usually found in the climax forest, were present in fair numbers in the screens 0.06 and 0.01, but were found in the other screens in very small numbers only.

Millipedes (Diplopoda) characteristic of soils of cultivation, and not of forest soil proper, were very abundant in the screens 0.5 and 0.2, and were rare in the darker screens.

Orthoptera, extremely rare as to either species or individuals, in the forests, were present in fair numbers in the lighter screens (Forficulidae, Acrididae—principally *Phymateus morbillosus*—Locustidae), but were almost absent from the darker. Forest Gryllidae, however, were more frequent in the darker screens.

In the instance of the Hymenoptera we note some interesting correlations. In the lighter screens there usually were throughout the year a certain number of flowers, and at particular seasons, masses of *Helichrysum*, *Ursinea*, and *Berzelia* blossom, whereas in the darker screens there either were no flowers at all, or at most, in light-intensity 0.06 a few flowers of *Stachys Thunbergii*,

*Lobelia* spp., and *Cryptostemma*. Accordingly we are not surprised to find that *Apis mellifica* and *A. caffra* visited the lighter communities frequently and in large numbers, while they failed to visit the darkest screen and but rarely were seen as individuals in the screen of intensity 0.06.

The scattered individuals of the genera *Anthophora* and *Xylocopa* behaved in the same manner, the flowers of *Virgilia* attracting them to the lighter screens; it must be explained that *Virgilia capensis* is an invariable constituent of all opener seral stages at Knysna.

Vespidæ and Eumenidæ sought the lighter screens, but the gall-forming Cynipidæ, true to their forest habits, avoided these screens and made their galls upon the foliage of the plants in the darker screens.

In the distribution of the Coleoptera some points of definite correlation were noted: the foliage-feeding Chrysomelids were more frequent in the darker screens simulating the conditions obtaining within forests, and were very rare in the opener screens, except on occasion, when they were found in the darker, weed-covered portions. The forms typical of forest soils were abundant in the darker screens, while the forms of cultivated soil were much better represented in the screens of intensity 0.5 and 0.2.

As in the instance of the bees, the Lepidoptera were almost confined to the screens of high intensity, doubtless on account of the presence of flowers.

Such Coccid colonies as occurred were upon the plants in the darker screens; the Coccids were identical with those found upon regeneration in climax forest; the few Aphids noted were confined to the lighter screens, on account of the presence of *Virgilia capensis*, the only forest plant seriously attacked as to the foliage by these insects.

Naturally the higher forms were not so abundantly represented—and this is readily understood to be a direct outcome of the smallness of the experimental sites. At the same time, the repeated presence from time to time of certain forms and the continued absence of others is well worthy of record:

Common frogs, while often noted in the lighter screens, on rare occasions only, appeared in the darker, but the forest frog (*Breviceps gibbosus*) not only was seen from time to time in the darker screens, but repeatedly was heard giving its peculiar call.

Owing to their being creatures of warmer brighter sites, the several species of lizard represented made their home under the weeds of the lighter screens; occasionally they were seen in the darker screens, but their presence there could be associated with the presence of large numbers of Diptera.

It may sound almost as exaggeration when I state that on several occasions large tree-snakes ("Boomslang," *Dispholidus typus*), inhabitants normally of the gloom of the climax forests, were found within the darkest of the screens, doubtless hunting for the occasional forest mice (*Mus* sp.) found therein. This may have been mere coincidence, but at the same time the occasional presence within the lighter screens of the small but highly poisonous, insolation-loving

Dik-kop adder" (*Bitis* sp. perhaps *caudalis*), and their absence, so far as observed, from the darker screens, is suggestive.

The few birds noted were true to their known habits: thus the ground haunting forest doves (*Haplopelia larvata* and *Chalcopelia afra*) were seen far more often within the darker screens. On the other hand *Dicrurus afer* "Drongo" or black bee-catcher) on occasion found his way into the brighter screens in search of bees, but was never noted in the darker. In customary fashion the ground-scratching Cape robin (*Cossypha caffra*), while a periodic visitor of the darker screens, on no occasion was seen within the brighter.

Observations upon mammals were confined to those on an indigenous forest mouse that sought food and refuge in small numbers in the darker screens, but steadfastly avoided the brighter, and upon the common *Mus musculus* that preferred to seek shelter within the weed cover of the opener communities.

As we later shall touch upon the matter of the place of plant parasites in natural communities, it may be said that the forest fungi of the orders Perisporiaceae and Microthyriaceae were better represented within the darker, forest-like communities, whereas the seral stage parasitic *Cuscuta* spp. and *Cassytha ciliolata* were represented in the opener communities only.

Reviewing this series of experiments, we see that particular habitat-complexes produced particular vegetation communities, and that these communities reacted in one manner or another upon the habitat. A vital difference in the factors light, temperature, and evaporating power of the air produced marked changes in a uniform soil, and together with these wrought distinctive changes in the nature and the species of the plants present; unquestionably the aerial, soil, and plant conditions attracted such animals as required those particular conditions. In the words of Yapp (57, p. 11) "the physical environment provided the stages on which the drama of organic life was enacted." But it may be added that it is an ever-changing stage!

Space and the hour do not allow of my giving even the all too sparse details known to me, of the conditions that obtain within the main seral stages in the development of the Knysna climax forest from the various types of Macchia, through the communities of *Virgilia capensis*, evergreen Scrub and evergreen Bush. The data suggest that while there are certainly stable forms that continue from stage to stage—for example, many species of soil protozoa, various insects and birds, and some of the smaller mammals, there are in addition marked changes in other animal associates as the stages develop. Specialised work, however, is required to throw better light upon this fascinating process<sup>1</sup>.

#### (b) *Biotic inter-relations in the forests.*

A few examples of the intricate co-actions among the plants and the animals may be of interest.

<sup>1</sup> Vide Phillips, "Forest Succession and Ecology in the Knysna Region." *Bot. Survey, Union of S. Africa Memoir*, 1931.

(i) Let us observe the far-reaching influences that the strand of earthworm numbers may have upon the general web of forest life. From experience it has been shown that according to the mean number of earthworms per acre of soil does the forest type vary. This to a large degree may be referred to the moisture content of the soil. The degree of soil aeration is an outcome of the reactions of the earthworms. Thus in a dry type forest (mean moisture content at 12–18 in.: 25–35 per cent. on dry weight) there are about 20,000 to 30,000 earthworms per acre. On account of the growth of much shrubby *Trichocladus*, and of the lactiferous lianes *Secamone Thunbergii* and *Ficus Burtt-Davyi*, and the occurrence of abundance of the relished foliage of *Pterocelastrus variabilis* and the bark of *Elaeodendron croceum* and *E. Kraussianum*, elephants are particularly partial to this type of forest. On the other hand, they are also attracted to the moist type of forest (mean moisture content 85–170 per cent.) produced upon soil of even lower earthworm numbers: from 15,000 to 20,000 per acre. The attraction in such forest are the ferns *Blechnum capense* and *Marattia fraxinea*, as well as the liane *Clematis brachiata*. The medium-moist forests (moisture content 45–60 per cent.), showing from 40,000 to 60,000 earthworms per acre, do not so much interest them.

When elephant frequent any portion of forest for any length of time, they are invariably followed by the scavenging *Potamochoerus choeropotamus* (wild pig), and at times by baboon, which take advantage of the roots and bulbs displaced by the great animals, and which are not above searching the droppings for food. The disturbance to the soil caused by the elephant, the wild pig and the baboon, brings about soil improvement, and stimulates many dormant seeds to germinate. Fruits passed through the animals are cleaned of their outer coverings and fall into improved germinating beds. Naturally a certain proportion of the fruits is spoilt in the process of passing through the animals, while existing regeneration may be destroyed.

We may push this matter of earthworm influences even further: it is that type of forest, the soil of which shows the greatest mean number of earthworms—the medium-moist type—that produces the best stocking of timber. Before the days of controlled exploitation—and, indeed, in privately owned forest to this day—this meant increased attraction for the wood-cutter. The effects upon plant and animal constituents of severe exploitation are outlined later.

(ii) We now turn to the matter of the inter-relations of plants with insects and higher animals, and select for example one of the most important insects, the honey-bee (*Apis mellifica*). Of the sixty-three more important trees and large woody shrubs of the climax forests, no less than fifty-two are pollinated almost entirely by honey-bees in the course of their searches for either nectar, or pollen, or both. Certain species—for example, the important and widely distributed *Platylophus*, *Cunonia*, *Apodytes*, and *Nuzia floribunda*—depend almost entirely upon the bee for their fruit crops. When the bees for any reason

are lower in numbers than normal, these trees and many others set poorer fruit crops than normal; conversely, until the introduction of many eucalypts and wattles to the district a few decades ago, the bees produced less progeny when, for any physical or biotic reason, the trees bore less flowers than normal.

The matter does not end here, however, for the bee has numerous enemies, among which the most potent native foes are *Dicrurus afer* (Drongo), *Oriolus larvata* (yellow bee-catcher) and *Mellivora ratel* ("Ratel"). Since the advent of the European the bee has acquired a new and even more ruthless enemy—the human honey-hunter, who destroys many young bees and "smokes" to death many adults. Nature deals in turn with the native foes of the bee, by means of the small Carnivores, *Herpestes* and *Zorilla*, while steps are now being taken by the Government to check the depredations of the human hunter. *Herpestes* and *Zorilla*, however, somewhat unfortunately for themselves, have increased to a considerable extent of late years through the gradual trapping and shooting of *Felis caffra* (wild cat) and the Cape leopard. They are, therefore, turning their attention to poultry, with the result that ultimately they will be much reduced, in turn, by man, and the bee-eating birds probably will once again increase considerably. Thus we see that the whole of the inter-relations is extremely delicately balanced; undue pressure in any one part of the web causes immediate reaction in every other part.

(iii) Our next duty is to consider a few cases of the influences of native insects upon native plants: *Olinia cymosa*, and especially *Olea laurifolia*, in certain years bear an extravagance of flowers, every year *Apodytes dimidiata* flowers richly, while *Ocotea bullata* flowers throughout each and every year. After admitting that the degree of successful fertilisation in *Olinia* is not high, and that, in *Ocotea*, this depends, *inter alia*, upon the proportion of hermaphrodite flowers produced (the tree is not visited by insect pollinators), we must nevertheless confess that the controlling influences of the Aphid that malforms a portion of the crop of *Olinia*, the Psyllids that cause wilting and death in a proportion of the flowers of *Apodytes* and *Olea*, and the Diptera and Lepidoptera that deposit their eggs in the flowers of *Ocotea* probably are wholly necessary for the keeping of a proper balance in the organic scale. The co-action of other animals is of importance in this connection: a small portion of the controlling influence of the insects on *Ocotea* fruits, for example, is nullified by several species of dove, the red-winged starling (*Amydrus morio*) and the fruit bat (*Rousettus collaris*) which, passing the fruit through their systems, thus remove the soft pericarps and with them the insects. The endocarps are deposited with the droppings, and certainly germinate more rapidly and to a much greater proportion than normal pericarp-covered drupes.

The woodpeckers *Campothera* and *Dendropicus* in their searches for the larvae of Scolytids, Longicorns and Cerambycids certainly relieve the boles of *Ocotea* and *Olea* of many disturbing insect parasites, but it is not perhaps known that these birds, through the abrasions they make and the spores they



carry upon their bills and feet, are very efficient distributors of parasitic fungi, particularly *Fomes applanatus*, a widespread agent of decay in *Olea*, and *Fomes hornodermis*, particularly partial to *Ocotea*. *Fomes applanatus* causes the fall of many a great tree of "Ironwood" (*Olea laurifolia*), and thus is indirectly responsible for the more rapid development of the regeneration surrounding the fallen giant.

(iv) Elsewhere (30) I have given details for the dispersal of fruits and seeds by the various birds and mammals. On this occasion I desire merely to point out that, in the Knysna forests, where the overwhelming majority of fruits and seeds are taken intentionally or by accident by birds and mammals, the influences of animals upon dispersal and in accelerating germination are indeed of incalculable importance in the life of the forest. The birds range from the diminutive *Zosterops* to the large *Lophoceros*, the mammals from tree mice to the Knysna elephant, and include several Carnivores that are capable distributors: *Felis caffra* (wild cat), *Herpestes* and *Zorilla* (so-called Muishonds).

(v) The importance of the rôle of lower plants in the life of the forests cannot be too clearly emphasised. I have given the details elsewhere, and now confine myself to recording that the fungi of the Perisporiaceae and Microthyriaceae unquestionably control, in many instances, the nature and the rate of development of particular forest regeneration and successional stages, and that such organisms as *Corynelia uberata* upon the fruits of *Podocarpus Thunbergii* Hook., *Pestalozzia* sp. nov. upon the drupes of *Ocotea*, and an unidentified fungus of the Hysteriaceae upon the drupe-stalks of *Olea laurifolia*, govern the output of fertile fruits. The action of *Fomes applanatus* in causing the fall of adult *Olea* has been mentioned previously.

(vi) Finally, we must touch upon the rôle of man, for his influences have become so ramifying that any study of the Knysna forests would rank as far from complete were his activities ignored.

Europeans have drawn upon the timbers of the forests since 1812, and for many years in a selective manner, the result being that to-day the proportion of semi-mature, mature, and over-mature individuals of certain valuable timber species to that of less-required or useless species is much smaller than formerly. Furthermore, through reckless felling and firing in the earlier days, man not only diminished the actual extent of the forests but produced marked changes within them. He has set train to innumerable examples of secondary successions—successions in which there are not only marked changes in the plant stages but also in the animals.

He has reduced one of the greatest animal associates, the elephant, from many thousands to a single small herd; by 1888 had annihilated another important animal, the buffalo; has made severe inroads upon the population of bush-buck (*Tragelaphus sylvaticus*), blue-buck (*Cephalophus monticola*), and grijsbok (*Pediotragus tragulus*); and has broken the power of the leopard. Mention has been made of his reduction of the honey-bee through ruthless

methods of honey-taking; but more recently he has, so far as the native forests are concerned, further reduced the bee population seasonally by the planting of extensive plantations of exotics extending marked attractions to the bee. His cattle browse upon the vegetation, but probably these by no means make up for the great herds of buffalo that he has exterminated.

The wilful or unwitting introduction of exotic weeds and other plants—for example, the British *Rubus fruticosus*, which has become a widespread and rampant noxious weed through its dispersal by native animals—in many parts has complicated the study of secondary successional development.

Throughout the all too cursory, and yet probably not especially lucid, account I have given of the inter-relations of plants and animals in the Knysna forests, runs the golden theme that the whole community of life is a beautifully integrated series of factors, responses, reactions, and co-actions. To remove the animals would result probably in dire results for the plants, to fail to include them in the concept of the community cuts across logic.

## (2) STUDIES IN THE GREAT EAST AFRICAN PLATEAU.

For further examples of the close inter-relations of plants and animals we turn to that wonderful, relatively undisturbed country, Tanganyika (late German East Africa). For the study of biotic communities this and other parts of east and central Africa are eminently suitable, owing to the comparatively natural conditions still obtaining. It behoves us to make use of our opportunities while this condition of things continues—in a few decades matters will have altered greatly.

### (a) *The general inter-relations of plants and animals.*

The vast concourses of animals in the savannahs of Tanganyika provide ready material for the study of the inter-relations, on a grand scale, of animals and plants. In the instances of certain animals—for example, the zebra—the herds consist of many thousands of individuals, while herds of several thousand antelope of single species may be seen in certain districts. Buffalo and elephant, if not in huge herds, are exceedingly abundant in many portions of the country, while lion and leopard are very well represented.

If we confine our attention to the principal animals of the Central Province of Tanganyika, we find the following actions of animals having a direct or indirect effect upon the vegetation:

(i) *The grazing and browsing of vegetation.* Chief among the grazing animals are zebra, buffalo, roan (*Hippotragus equinus*), hartebeest (*Bubalis Cokei*), impala (*Aepyceros melampus*), waterbuck (*Kobus ellipsiprymnus*), reed-buck (*Redunca arundinum*), and blue wildebeest (*Connochaetes taurinus*).

The important browsers are giraffe, elephant, rhinoceros, bushbuck, wild pig (*Potamochoerus*), and wart-hog (*Phacochoerus*), and among those that both graze and browse are the greater kudu (*Strepsiceros*), the lesser kudu (*Ammelaphus imberbis*), and eland (*Taurotragus oryx*). In this class elephants too find a place.

When these animals—and the host of less-important forms that cannot be mentioned—are present in abundance, the effects upon the plants are remarkable. For example, the removal of the older grass from the perennial roots and tussocks undoubtedly stimulates the production of better growth the following season—a point that the work of the Biological Survey of the United States has shown to be of real importance in grazing management. Again, the selective browsing of species of grass and of herbs and shrubs, and the regeneration of trees gradually alter the balance of species in successional stages. Repeated browsing of shoots either inhibits growth or results in the development of shrubby, much branched forms. Wood-dwelling and wood-eating termites control the length of life and the numbers of many species, and definitely prevent the establishment of others.

(ii) *The action upon the soil.* A study of the soil surface and texture in areas where there are hosts of animals immediately shows that profound influences are wrought in the texture, in the degree of aeration, and in the chemical conditions of the upper portion of the soil, as the result of the tossing by the horns, the trampling by the myriad hoofs of gambolling, grazing or lion-driven beasts, the rolling of a thousand forms and the deposition of many tons of manure.

But more, we must remember the underworld of the steppes—the hosts of delvers and burrowers, the uncountable hordes of subterranean gallery-makers. Chief among the forms of the underworld are the ant-bear (*Orycteropus*), the scaly ant-bear (*Manis*), *Pedetes*, *Tatera*, *Heliophobius* and a great fauna of other rodents. Some part too is played by the wart hog and the wild pig. Mighty in their extensive and intensive work of gallery making, soil aeration, and formation of humus are the numerous species of termite. In the great chambers formed by some termites, often live mongoose and rodents. Formosov (23, p. 459) describes similar conditions for the steppes of southern Russia and northern Mongolia.

In connection with the influence of the subterranean animals I may refer you to the interesting work in the United States, of Taylor and others, of the Biological Survey, in which is clearly set forth the value of the work of pocket-gophers, kangaroo rats and ground-squirrels in soil improvement (45-50).

(iii) *The dispersal and destruction of fruits and seeds.* An examination of the droppings or of the stomach-contents of forms ranging from the elephant, the rhinoceros and the buffalo through the antelopes, the smaller Carnivores such as the civet, and the smaller species of *Felis*, and the Primates, to the birds, shows that in East Africa, even as at Knysna, the dispersal of many species of fruit is through animal agency. Undoubtedly considerable destruction takes place during the passage from snout to vent, but equally undoubtedly is germination in many species much accelerated by the passage. Frequently distributed seeds are those of the Acacias, Cassias, the tamarind, Albizzias and other legumes, the Commiphoras, Grewias, the species of *Strychnos*, *Balanites*, *Royena*, and *Ficus*, and the baobab, *Adansonia digitata*.

(iv) Man through the ages has played a mighty part, not so much through the practices of agriculture, which have produced erosion and thus set train to new successions of plants and animals, but through the agency of the annual grass fires<sup>1</sup>. Indeed these universal fires have become a definite feature of the dry season; apart from their checking influences upon the young of animals, they have succeeded in holding in check certain stages of the successions—thus the opener communities, including the *Berlinia-Brachystegia* Woodland of the Central Plateau, undoubtedly are inhibited from developing to the scrub climax by the annual or biennial fires.

Again, we see the complexity of the inter-relations, the clear inter-dependence of plants and animals.

(b) *The inter-relations of plants and animals in the ecology of the tsetse fly*  
(*Glossina morsitans* Westw.).

But we have yet a more striking example of the necessity for thinking in terms of plants and animals living together—that of the tsetse problem, and particularly that problem set by *Glossina morsitans*, which in common with other species of the genus is an important vector of trypanosomiasis in man and beast. Indeed, in my experience, there is no biological problem that more lucidly sets forth the truth that we must think in terms of biotic communities and not of isolated plant or animal assemblages.

In the space available I shall endeavour to describe some of the co-actions exemplified in the ecology of *G. morsitans*.

Within the limits of its distribution in sub-tropical and tropical Africa, this species of *Glossina* generally is found within regions of undulating plains and hills. The soils of the plains may be either alluvial or residual, but the soils of the hills are invariably residual, and often show profusion of rocky outcrops.

Upon the plains occur vegetation communities that fall naturally into the following general categories: (i) Open Grassland—the East African “mbuga” if on alluvial soil with or without a scattering of shrubs and trees—these woody growths being inhibited in their development by the ever-recurring grass fires; (ii) *Acacia*—Open Woodland with extensive grass, short or long; (iii) *Combretum*—Other Species Open Woodland, with extensive grass strata; (iv) Deciduous or very largely Deciduous Scrub, chiefly formed by the genera *Commiphora*, *Grewia*, *Acacia*, and members of the Rubiaceae and Capparidaceae; this Scrub may be either very dense or may occur as islands of variable density in other communities. It supports either no grass or a very sparse, interrupted cover. These communities, in Central Tanganyika, are related stages of the succession ending in the Deciduous Scrub climax.

The hills that follow each other as so many waves of the sea, carry league

<sup>1</sup> Vide Phillips, *S. Afr. Journ. Sci.*, **27**, 1930, for an account of the influences of fire upon biotic communities in South and East Africa.

upon league of one of the most extensive vegetation communities in Tropical African savannah—the *Berlinia-Brachystegia*-Other Species Woodland. Successional to Deciduous Scrub, this woodland of widely spaced grey-barked trees, largely leguminous, is kept from developing to Scrub largely through the agency of fire. It is found upon residual soils only.

The severity of the aerial and soil conditions increases as the *Berlinia-Brachystegia* Woodland is left for the opener communities—and more especially is this so during the dry season when the foliage has fallen. Apart from the Scrub, which is highly unattractive to game on occasion of its tangled nature and the almost complete absence of grass, the *Berlinia-Brachystegia* Woodland gives aerial conditions slightly less bright, hot and dry than the opener communities.

From time to time, especially upon situations above 4500 to 5000 ft., there is found the seral *Brachystegia microphylla-Berlinia*-Upland Woodland—consisting of larger trees than the *Berlinia-Brachystegia* Woodland, and showing many of the regal *B. microphylla*, which is usually poorly represented in the *Berlinia-Brachystegia* Woodland.

In the Kondoa-Irangi region the game during the rainy season (December to May) is generally distributed throughout all the opener communities, and largely finds its home in the great open grass areas or “mbuga.” During the dry season, however, when water is to be found either in a few perennial streams or water-holes, largely in opener communities upon alluvial soil, the game and the principal associated Carnivores, lion, leopard, and hunting dog, aggregate within short radii of watering places. The grazing within such vicinities is usually attractive at the same time. While game may be found from time to time in the *Berlinia-Brachystegia* and the *Brachystegia microphylla-Berlinia* Woodlands, in both dry and in rainy seasons, they infinitely prefer the open communities—on account of better grass, better visibility assisting them to steer clear of lion—and proximity to water.

As the tsetse—so far as we can argue from the absence of carbohydrate-digesting enzymes (56)—is entirely blood-sucking, it is not surprising that the movements of game have an appreciable effect upon its habits. For example, the work of my colleagues Dr Nash and Dr Jackson has shown the following points of interest:

In a region where the opener communities or grazing grounds are extensive, the game population great, the movements of that population on a grand scale with the seasons, and the fly abundant, it seems that game movements produce effects in the number and constitution of the fly population; that a concentration of game causes a large increase in the fly density-activity in the surrounding country; and that when the game disperses the density-activity of fly again decreases. A marked increase in the proportion of female tsetse accompanies the concentration of game. Around water-holes where game congregate, dense fly “centres” form, and may continue for some time after the game has dispersed.

On the other hand, in a region where the grazing is confined to small glades set in a matrix of denser vegetation, where the game population is relatively sparse, and the fly numbers medium to low, somewhat different results are produced. According to the observations of my colleague Dr Jackson, such relatively local grazing areas—usually grassy “mbuga” successional to Scrub, and perhaps showing a water-hole for part of the year at least—are highly attractive to game. The *Berlinia-Brachystegia* and *Brachystegia microphylla* Woodlands that ascend the slopes and cover the tops of the surrounding hills, and the *Combretum*-Open Woodland interspersed with Deciduous Scrub, are much less attractive. The outcome is that at the grazing and drinking sites there are built up centres of tsetse, which show a much higher proportion of female fly than does the population of the surrounding vegetation communities; furthermore they show a high proportion of young fly. The fly population of the *Berlinia-Brachystegia* Woodland, however, shows a very high proportion of male fly, females being almost completely absent. And now comes the point of importance—the fly of the centres in the open glades are fly anxious to feed—they are hungry fly; this is known from an examination of the abdomens of the fly, from the fact that young, therefore hungry fly are present, and from the appearance of large proportions of females, which do not show themselves unless they are either hungry or desire to mate. The fly of the *Berlinia-Brachystegia* Woodland, however, are replete fly, or fly not yet sufficiently hungry as to desire to proceed to the glades. From some observations by Dr Jackson, it seems as if the fly of the vegetation transitional from the open glades to the *Berlinia-Brachystegia* Woodland are a mixture of hungry fly proceeding from the woodland to the glade, and of replete fly proceeding from the glade to the woodland.

From these two instances of correlation between game and fly, we see that the keynote is in reality the vegetation type: vegetation type presents particular features favourable or the reverse to game, and the fly associates itself with the vegetation type and thus with the game.

From data supplied by my colleague, Dr Nash, it is suggested that in a region rich in game during the rigours of the dry season, the physical conditions induce the fly to leave the opener, severer plant communities, to take shelter in the less severe woodland of *Berlinia-Brachystegia*, from which they sally from time to time to the opener types for game. Conversely, from Dr Jackson's evidence, it is conceivable that in a region in which game is especially sparse in the late dry season, the fly has to spend more of its time in the opener types—searching for game.

Vegetation plays so important a rôle in the ecology of game and fly that it has been possible for Messrs Nash and Jackson, on the basis of quantitative samples over a long period, to classify the fly-preferred types in the regions in which they are working. In the Eastern Fly Belt of Kondoa-Irangi the fly seems to prefer the types in the following descending order: (i) *B. micro-*

*phylla* Woodland; (ii) *Acacia usambarensis* Woodland; (iii) *Berlinia*-Other Species Woodland; (iv) *Combretum*-Other Species Open Woodland; (v) *Acacia spirocarpa* Open Woodland; (vi) *Acacia formicarum*-*Ac. Seyal* Open Woodland; (vii) large areas of open or almost treeless grass; (viii) native cultivation.

In the Western Fly Belt of the same region, the fly prefers the following in descending order: (i) *Berlinia*-Other Species Woodland, and closely-stocked woodland of *Acacia spirocarpa*; (ii) *Acacia stenocarpa*-*Ac. Senegal* Open Woodland; (iii) Open Woodland of *Acacia Kirkii* and *Ac. Rovumae*—very variable, depending upon the surrounding types; (iv) Deciduous Scrub, from which it is almost or entirely absent; depending on the density of the vegetation.

Man comes into the biotic community at times: for example, he is driven by advancing human or cattle trypanosomiasis from his villages, with the result that vegetation rapidly develops upon his gardens and grazing areas, game advances, and with it the fly. On the other hand, he may be living within a vegetation-cleared area sufficiently large to inhibit the advance of fly, but may be prevented from grazing his increasing stock in the adjacent woodland, on account of the presence therein of tsetse. The outcome is overgrazing with concomitant sheet and gulley erosion, a process that sets train to new stages in plant and animal successions. Finally he may remove vegetation, drive out the game, and thus upset the equilibria for the existence of tsetse.

Reviewing the story of the inter-relations in the ecology of *G. morsitans*, it is seen that there is a wonderful web linking and interlinking the physical factors, the plants, the game, the tsetse and man himself, a web of the most intricate spinning of woof and warp. Alteration in the tension of any single strand is immediately transmitted to a magnified degree throughout the web.

## V. CONCLUSIONS.

Reviewing the literature and my own experience in the study of communities, I am of the considered opinion that the concept of the community being *biotic*—constituted by inter-dependent organisms with integrated responses, reactions, and co-actions—is the most logical and by no means the least practicable of the concepts.

In the biotic community I should include not only the higher plants and all forms of animal life—including man himself—but would also give place to those apparently insignificant but in reality influential organisms, the cryptogams. My inclusion of man doubtless will call for much criticism—so to anticipate such I would remind you that despite the ability of man to upset temporarily, to hold in check to some degree, and to accelerate to greater or lesser extent the responses, the reactions, the co-actions and the development of a community, it is more than he can do to alter fundamentally the trend of these. To him certain—and not all—things are possible.

Nature's spread page, when earnestly and critically studied, reveals more

and more clearly that she functions in terms of biotic communities. Where we find it difficult to understand her in this connection, it is not because she is either ultra-obscure or inconsistent, but rather due to our inherent lack of knowledge and perspective, a lack that time and perseverance alone will partially satisfy. At all events we shall not find her working either in isolated plants or in isolated animal communities. To consider either plants or animals as factors external to a community can but continue to curtail our knowledge of the inter-relations of the several forms of life.

It is in keeping with the importance of the subject that I should at this juncture refer to a further aspect of the community—that aspect that has already called for criticism from certain quarters—the community as a *complex organism*. Clements (8, p. 199; 10, p. 3; 16, p. 314) in his purpose of introducing the term and view appears to have been misunderstood by some (18, 24), but has had the support of Tansley (41, p. 123; 43, p. 678) provided the term *quasi-organism* is employed and provided the concept applies to Tansley's *autogenic succession*<sup>1</sup>. Briefly Clements's purpose is to emphasise the organic entity of the community, his epithet *complex* immediately distinguishing this *communal* organism from the *individual* organism of general terminology. While I—and doubtless Clements himself—would agree that philosophically General Smuts (40, pp. 339–43) by his masterly and inspiring exposition—in a universal connection—that groups, societies, nations, and Nature are *organic without being organisms*, are holistic without being wholes—has pointed to the truth, I still am able to see that the concept of the *complex organism* has much to commend it in practice. It certainly focusses attention—and such a focussing is essential to advance—upon the place and function of all life in that organic entity the community.

The reactions of a stand of plants is more physically than the sum of the reactions of each of the separate plants; the reaction of the biotic community more than the sum of the reactions and co-actions of the constituent plants and animals. This something more is represented *inter alia* by the aggregate shading, alteration in temperature and rate of evaporation, the improvement of the soil, and the responses of the plants and animals themselves. A biotic community in many respects behaves as a complex organism—in its origin, growth, development, common response, common reaction, and its reproduction. In accordance with the holistic concept of Smuts (40), the biotic community is something more than the mere sum of its parts: it possesses a special identity—it is indeed a mass-entity with a destiny peculiar to itself.

<sup>1</sup> Through the courtesy of Prof. V. E. Shelford (38, p. 4) I have been able to consult the manuscript of his paper "Some concepts of Bio-ecology" in which he likens the biome to an amoeboid organism, a unit of parts, growing, moving, and manifesting internal processes which may be likened to metabolism, locomotion, etc., in an organism. Forbes (22) says, "A group or association of animals or plants is like a single organism in the fact that it brings to bear upon the outer world only the surplus of forces remaining after all conflicts interior to itself have been



Criticisms that may be levelled at the concept of the biotic community are that at times no correlation between the stages of the plant succession and the animal population is to be found, and that animals range from plant stage to plant stage. I suggest that as our knowledge increases we shall find that despite the linkage in certain instances of animals to plants which are relicts of an earlier stage, despite the wide-ranging predilections of certain forms, there are, definitely, forms that are peculiar to stage, and that the ranging forms probably play a part in some special seasonal or other aspect of certain stages.

Unquestionably the logical basis of classification of the biotic community is development, for this basis alone enables us to refer the present to the past, and to point the present to the future.

As the dominant plants not only give physiognomy to the community, but provide protection, shelter, breeding sites and food to the animals, and as the influence of the more important animals will take some time to decide, the first step should be to base the nomenclature of biotic communities upon the dominant plants. Upon the reactions and co-actions of the predominant animals being decided, the names of one or more of these might be added to the name of one plant dominant or to the names of several plant dominants. Such details, however, may readily await our gaining more experience in the study of biotic communities; *we should not endeavour to lay down rules at this stage.*

## VI. METHODS.

I can scarcely leave unmentioned the matter of methods likely to be of utility in a study of the biotic community—but at most I can here but limn the outline.

At the outset it must be realised that students aspiring to be ecologists should receive a broader training in biology and the physical sciences, and above all should be trained in practical instrumental, quadrat, and animal sampling methods. To my mind an excellent setting for this after-training is a course in either agriculture or forestry for the worker who is to deal with general problems, and a course in either veterinary or medical science for him who is to study specific biotic problems regarding animal and human welfare<sup>1</sup>.

Secondly it seems plain that co-operative or team work is essential; botanists, zoologists, workers in other sciences must labour together, and link up with the men of practice and administration. The field is too wide for any single worker—the investigators of the biotic community must be inspired “to set the cause above renown, to love the game beyond the prize”—a sentiment as yet none too common in circles ecological<sup>2</sup>.

<sup>1</sup> These views were stressed by myself at the Imperial Botanical Conference, in London, on 15th August, 1930.

<sup>2</sup> Through the kindness of Prof. W. C. Allee (4) I have been able to consider the manuscript of his address, “Concerning Community Studies.” By taking as a hypothetical example the study of the biotic community presented by the University of Chicago staff and students, he lucidly urges the inherent inefficiencies of our present methods for the study of communities of organisms.

Essential lines for practical investigation are: (i) Primary surveys of the important plants and animals of natural regions—these surveys would suggest the most effective lines and the most suitable sites for investigation of development and its causes<sup>1</sup>.

(ii) Developmental studies within important stages, by means of instruments, quadrats and quantitative animal samplings (*vide* Phillips, 34).

(iii) Special habitat simulation experiments by means of controlled natural or artificial environments; these would throw light upon prime responses, reactions, and co-actions.

Details for the investigation of the biotic community in the tsetse problem are given by myself elsewhere (33).

#### VII. APPLICATIONS.

Unquestionably the study of the biotic community would reveal information of fundamental economic value in various fields. For example, in *forestry* it should elucidate problems in silviculture and forest regeneration, it should enable *agriculturists* to select and manage the crops of a region with improved results, *grazing* policy and management would increase in efficiency as the inter-relations of wild or domesticated animals and pasturage are better understood, while *economic entomology* would find its knowledge of pest control assuredly enriched as it investigated the basic interdependence of plants, insects, and other organisms. In specific instances—to wit, trypanosomiasis, plague, malaria—human medicine could learn much from an application of the concept of the biotic community.

Lastly, I have faith that through steadfast investigation of the organisation and life of the biotic community, we, with painful, slow but not uncertain steps, would draw a little nearer an interpretation of that grand riddle—the ecology of the Universe.

#### VIII. SUMMARY.

1. An attempt is made to outline the views of ecologists regarding the relations of plants and animals in natural communities. These views are considered under the heads: (i) Animals as biotic factors external to the plant community; (ii) Animal communities to which the plants are a portion of the habitat; (iii) Biotic communities—made up of interdependent plant and animal members.

2. Examples of inter-relation and inter-dependence in natural communities are given from the writer's experience in the sub-tropical evergreen forests of the Knysna, South Africa—data being given from experimental and observational sources. In addition, he records the inter-relations of plants and animals in the savannah regions of East Africa, drawing examples from the great game fauna, and from the ecology of the tsetse-fly, *Glossina morsitans*.

<sup>1</sup> *Aerial survey* with supporting ground reconnaissance would be especially valuable in the investigation of the tsetse problem in the best known regions.

3. It is concluded that the most logical working concept is that of the biotic community. Furthermore it is held that Clements's view of the community being a *complex organism*, while philosophically perhaps not wholly true, has definite practical value.

4. A very brief outline of methods, and of the applications of the concept, is given.

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## AN ECONOMIC ASPECT OF REGIONAL SURVEY

By C. R. ROBBINS.

(*With Plates I-III.*)

THIS article is mainly devoted to the development, on a large scale, of the application of ecology as an essential preliminary step to the formulation of a well-laid plan and policy for a "new" country. Such development of the science of ecology naturally proceeds along two lines: that of overcoming the natural obstacles that are inherent in mere size and bulk and that of securing adequate and intelligent co-operation among all the sciences and arts involved. This "rationalisation" has long been a feature of what may be described as academic ecology, where the individual scientist has realised that he must call for assistance and advice not only from members of sciences of which his own knowledge may not be profound, but also from those of his own particular interest. The problem, however, becomes complicated immediately practical results on a large scale are required because so many interests become involved, personal, industrial, government, etc. While it is realised that with the great responsibilities and issues involved it is difficult to avoid the "cubicularity" of the various government departments, it is believed that a method has now been evolved whereby the rationalisation of science and industry and government can be extended to include all three. To explain this method is the primary object of this article.

The problem for an undeveloped country boils down to one of finding what that country contains, and how such contents, potential or actual, living or dead, can be got out. To ascertain this on the wide, general lines essential, it is necessary that all the departments of the local government shall co-operate, and that they shall have at their disposal the latest scientific knowledge and methods. Primarily there will be required maps (topographical, geological, edaphical and vegetational), and from these will arise a demand for further information over certain areas; bigger scale maps for railways, roads, pipe-lines, etc.; mineralogical maps and maps showing areas suitable for forest only, and those suitable for various kinds of agriculture and for irrigation or draining. The old method of each department producing annually, with its limited staff, and quite independently of what other departments were doing, so many square miles of new map, topographical, geological and so on, is not only entirely wasteful owing to overlapping, but by its slowness prevents any general policy and plan of development being formulated. The solution would appear to lie in the use to the utmost of any new method which can permit of co-operation with the local officials, can provide all the information

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quired at one time, and can call on the results of the very latest scientific investigations to assist in its compilation.

Such a method is already available, and lies in the use of the aeroplane with a full complement not only of experienced pilots, observers, and photographers, but of specialised geologists, soil-scientists, surveyors, agriculturists, foresters, botanists, etc. It cannot be too much insisted that air survey no longer consists of "splashing" a few photographs over an area and sticking them together, but has become an exact science with its own particular technique, machines, and instruments. And just as for the preparation of an accurate topographical map by aerial methods adequate ground control is essential, so for the other purposes a staff of trained scientists must be employed. The great advantage of the combination is that complete co-operation is secured and all concerned, whether on the ground or in the air, will be working together to a common end.

The adequacy of the air method for producing topographical maps of various kinds and scale has been fully demonstrated. The results achieved in vegetational and forest stock maps, whether by the use of photographs or by visual reconnaissance, have also been sufficiently shown. The project of producing at one time a complete reconnaissance map showing not only topographical features, but the "regions" and the various geological and ecological formations, is, however, revolutionary, and as such is naturally and rightly open to trenchant criticism. Such comments can come mainly from two directions: from those who deny the ability of the air method allied with adequate ground control to produce the required information; from those who doubt the importance placed on co-operation and the employment of a special staff to achieve it. It is true that these criticisms cannot be met by the best of all arguments: a full-scale successful example of the process in operation. Were it so there would be no necessity to make an effort to prove the case. But every new process that really marks an advance must pass through its experimental tests, and no better place could be found for such tests than an area where all information supplied by this new method could be checked by reference to accurate and existing knowledge. Such areas can be found almost anywhere in England; the actual part chosen for this demonstration consists of a strip running across the southern middle part of England from some miles north-west of Oxford to near Marlow. This was chosen because it is easily accessible, and many geological, soil and vegetational changes are encountered. The actual selection of the area was made by Mr R. Bourne of the Imperial Forestry Institute, who has for some years been interested in this new application of the aeroplane to old problems. Pioneer work of this nature, which is of particular interest to geologists, soil scientists, ecologists, agriculturists and foresters, and is of general importance, needs recognition and, more especially, assistance in the form of funds and expert help. Mr Bourne alone expects to achieve the results which

would be obtainable given adequate co-operation with the various specialists concerned. His investigations are not yet complete—and it is hoped they never will be, as fresh potentialities become visible—but they have proceeded far enough to give definite results and nearly all the following statements are based on his research work.

Two examples can be quoted as answer to any question as to the necessity for close co-operation between all concerned in any comprehensive survey: one from overseas, showing the overlap that arises when each part of the survey is done separately, and one arising as a direct result of Mr Bourne's work.

The first example is taken from the part of Lower Burma known as Tenasserim. This area comprises some 16,000 square miles; is largely covered with dense evergreen forest; and has a small population, most of which is concentrated along the coast. After many years of inactivity the area was mapped on the scale of 1 in. = 1 mile, but no attempt was made at that time to secure any geological or forest data, both important in an area heavily mineralised and mainly tree-clad. Soon afterwards the geological department sent out its surveyors and they prepared excellent maps showing the main geological formations but without indication in any way of the soil and agricultural possibilities of the hinterland. Finally the forestry service undertook a complete survey to prepare stock-maps of the various forest types: these maps certainly achieved their main object, that of showing those areas worthy of permanent allotment as reserves and those which contained poor stands.

But all these uncoordinated effects, while each produced excellent results in its own way, failed to correlate the geological, soil, climatic and other factors that gave rise to the existing state of things. If all the operations had been carried out together with all concerned in close co-operation a "regional" map might have been prepared which would have shown the locations and areas of the regions of different potentialities. In such a forest belt it does not follow that areas bearing good forest stands are necessarily "forest land" nor that those with poorer tree crops should be excluded from forest reservation. Moreover, it is wrong to assume that a geological formation will produce the same soils over its whole area, or that the soils from two different rock formations may not be identical from the vegetational point of view.

And this immediately leads to one of Mr Bourne's contentions, namely, that the "solid" geological map, as generally prepared nowadays, however accurate it may be, can be quite useless for determining the area and situation of those overlying soils that are suitable for agriculture. Even "drift" maps are, in many cases, quite inadequate. His research has carried him across a very varied series of rock near Oxford: he has encountered Great Oolite, Forest Marble, Cornbrash, Oxford Clay, gravel terraces, Calcareous Grit, Coral Rag and Kimeridge Clay. These are the formations as marked on the 6-inch geological map and, considering the largeness of the scale and the accuracy of the survey, it might appear to be a logical deduction that, in most

cases, the surface soils would bear a fairly close relationship to the underlying beds. But this is frequently not so, and for four reasons.

Firstly, the classification of geological formations is based largely on fossil evidence, and little or no discrimination is made between different beds within the same formation. For example, according to the weathering and physiography, Forest Marble may outcrop on the surface as a brashy limestone or as a clay; and the Kimeridge Clay may be covered in places by a cap of sand of the same formation that, in other places, has been washed away. Yet even the "drift" map will show only Forest Marble or Kimeridge Clay in spite of the great soil differences involved.

Secondly, the purpose of the geologist being to prepare a map of the main formations, he is naturally apt when encountering outliers, or at the transition zone of his formations, to disregard outcrops that do not show a depth of at least a foot or to draw back his boundaries until some such depth has been found. Soil mapping not being his business, his geological map may present an entirely false impression to the farmer or forester, to whom the top few inches or feet are all important. Moreover, the personal element enters and in some places quite thick caps may be disregarded, while in others the boundaries may be carried to the extreme limit.

Thirdly, no attempt is usually made to show any local "creep" or movement (apart from folding) of one rock over another, and the creep, for example, of a cap of calcareous grit over Oxford Clay or of Kimeridge Sand over Kimeridge Clay is completely ignored, although it may completely change the soil conditions where it occurs.

Fourthly, unless special "drift" maps have been prepared the full extent of glacial "drift" is not shown and even six inches of such "drift" may altogether alter the potentialities of the soil.

The above examples do not embrace a large area, and the rocks concerned are all sedimentary or alluvial, but additional evidence is becoming available in the continuation of the area to the east, through the Greensands, Gault, Chalk, etc., and such discontinuous formations as the Bagshot Sand to the London Clay. Although the area is small the change of formation is very frequent, and it is considered that Mr Bourne has proved his points that:

(1) Geologists should map the beds to their extreme limits including the "creep" and the full extent of drift.

(2) If they will do this and will discriminate between different beds of the same formation, soil mapping, whether according to profile or texture, is for all practical purposes finished.

(3) But to do this within reasonable time they must have botanical knowledge, or co-operate with botanists, for the recognition of plant indicators to obviate an enormous number of borings or sections.

If the above contention, namely, the necessity for intensive co-operation, is accepted, it still remains to demonstrate the use of the aeroplane



in assisting the promotion of such combined surveys over wide areas. It is to this point that all Mr Bourne's researches are now leading, and it is considered that he has here also successfully proved his thesis. At first sight, from the air view, no more unpromising and less differentiated area than that chosen could have been selected. To an untrained observer flying over the country there would appear at the most agricultural lands of mixed pasture and arable, diversified with pine, beech and oak woods, and if the problem had been attacked from this end it is probable that no definite scientific results would have been obtained. But the work was approached through investigation on the ground itself, and apart from the use of aerial photographs (which provide the only maps that can show *all* the superficial features of the country) no heed was taken of the employment of aeroplanes, whether photographically or visually, until the ground data had been established. The following sequence gives the order of the different operations in thought, but not necessarily in deed, as many could, and normally would, be carried out at the same time.

First, a soil map was prepared by actual borings. For this the geological map was of assistance, but, as stated above, could be definitely erroneous or misleading where soil features were required. Second, there were noted for each soil type particulars as to the configuration, form of agriculture, crops, natural vegetation (species and growth), etc. Third, a study of each soil type was made as to which, if any, of the foregoing features and of any others would be distinguishable from the air, either visually or photographically. Such features would again include the form of agriculture and the crops, but would also embrace presence or absence of woodlands; species and growth of trees; shape, size and colour of fields; presence or absence of hedges, stone walls, ditches, etc.; the configuration and general appearance of the countryside. The last feature may seem very vague, but it must be remembered that literally a bird's-eye view is obtained and that once an observer knows his type he recognises it elsewhere by all the above indications combined *plus* an appearance, diverse from that of other types, which it is difficult to analyse and split up into its various, frequently very small and numerous, causes.

The regions having been discovered and their ground and aerial features analysed there only remained to see whether the regions could be recognised from air photography or visually. Little difficulty was encountered in this, and where there was considerable risk of confusion between two superficially similar regions overlying different rock formation, e.g. Kimeridge Clay and Oxford Clay, the correct choice could probably nearly always be made on the evidence of the adjoining regions. It is admitted that a good deal of the evidence on which the aerial decisions would have to be made is, in this instance, artificial and such as would not be encountered in an undeveloped country. But it is contended from experience that the natural superficial evidence supplied by such a country would be much easier to read as it more directly

affects the factors and is not an indirect product of these same factors acting through man. Moreover, it is improbable that the many changes of region found in this experimental strip would normally be encountered in areas not specially selected for such changes; larger, well-differentiated blocks are more probable. The combined survey with which this article mainly deals will find its greatest scope in undeveloped countries for which a concerted plan of development is urgently required. Countries fulfilling these conditions are to be found in many of our African dependencies, where not only is there necessity to discover quickly the mineral, agricultural and forest resources, to decide the best lines for rail and road construction, and to allot the lands for forests, agriculture, etc., on a scientific basis, but there exists the prime urge of allocating the territory to natives and immigrant Europeans in such a manner that shall be satisfactory to all concerned and shall be permanent.

For such a country the procedure of the survey would be roughly as follows. The whole area would be rapidly covered with oblique photographs for the preparation of a small-scale reconnaissance topographical map. While this photography was taking place the ground surveyors, geologists, interpreters (i.e. aerial observers and readers of aerial photographs), etc., would determine the best lines for strips of vertical photographs to be taken. These strips would be used to "tie-in" the obliques and would be used as maps by the aforesaid ground staff. The ground staff would then proceed along the lines of these vertical strips and each member, while in co-operation with the others, would carry out his own particular work. The ground surveyor would fix his control points (astronomically or with a theodolite) and the others would gather all available information as to the geology, soil, forests, etc. As soon as this information permitted the determination of the various regions the chief interpreter could train others less skilled than himself in identifying the various regions on the ground by their superficial features without knowing the why and wherefore. He himself would return and from a study of the photographs or by visual reconnaissance would mark on the small-scale maps the boundaries of the various regions. Those regions which appeared to lend themselves more fully to development would then be covered completely with vertical photographs, and a much fuller ground control would be started embracing all phases, topographical, geological, vegetational, etc., with a view to the preparation of large-scale maps with more information. As such works progressed still bigger scale maps and still more information would be required about certain areas until the final situation would be a practically complete knowledge of areas wanted for immediate development, fairly full knowledge of other areas potentially valuable but not immediately required, and a general knowledge of the remaining and less valuable districts.

To sum up, the main points are:

1. A realisation that the aeroplane, its camera and the observer's eye are merely new instruments, and that the whole work depends on a specialised

scientific ground staff who must combine in every direction. The function of the air part is to apply the ground knowledge and thereby gain speed and save cost and to produce "regional" as opposed to merely local results.

2. The extraordinary amount of local knowledge that can be acquired in a short space of time as a result of systematic ground survey by a trained staff. The point will be appreciated by forest working-plan officers who usually, on the completion of their systematic field work, know more of the real status of the forest than the forester in charge who has been largely occupied with administration. It is also apparent in the knowledge gained by a soil scientist in a very short time as compared with the farmer's acquired experience. It is indeed comparable to the topographical map prepared in a limited time by a proper surveyor and the sketch filled up from time to time by untrained individuals from haphazard traverses, measurements, hearsay, etc.

3. The manner in which such surveyors pave the way to an understanding of vegetational succession and help the botanist and forester to differentiate between the respective effects of local factors and of man on the existing vegetation.

4. The extent to which systematic surveys throw light on controversial questions of agriculture and forest practice and help to clarify the issue. Most of such controversy is due to insufficient premises and evidence.

5. This article gives a very general account of the processes involved and the objects sought. The publication of Mr Bourne's full description and his approach to the subject, the methods employed and the results achieved will be awaited with great interest.

Most of the references in this article have so far been directed to the application of the methods involved in the study of actual or potential agricultural lands. But during the process of the ground work it has become increasingly apparent that this approach has direct bearing on the cultural problems of the forester. Most modern forest working plans; on the Continent, in India and the Dominions and in the United States; are based on a stock-map of the forest types, an estimate of the volume, or an equivalent, and consideration of price and methods of exploitation. Such are essential, but the tendency has been rather to make the cultural ideas fit the results produced by consideration of management. A compromise is usually inevitable, and every forester knows that to maintain the yield he should know how he can regenerate an area before he starts removing the existing crop. The soil surveys carried out, in combination with the knowledge of the state of the crop, growth, and regeneration on the spot have shown a very definite correlation between the appropriate silvicultural system and the site factors. To introduce the proper cultural treatment to every site may entail great complications over quite small areas, but any sequence of sites is likely to repeat itself again and again throughout a whole forest unit so that actually the same

## *An Economic Aspect of Regional Survey*

umber of silvicultural systems may be required, although these will be applied locally and correctly over many small areas instead of in blocks and mainly over a few large areas. Correct soil maps are thus seen to be as important to the forester as to the agriculturist. Moreover, although the evidence so far scanty, it appears that the aerial method may assist in fixing the area for different treatments. In the beechwoods and plantations of the Chilterns those localities where the beech is dying back on certain chalk lands, or where parts, or the whole, of plantations have failed, can be seen in air photos and can supply evidence as to the soil factors or *vice versa*, once the correlation is known.

### DESCRIPTION OF PLATES I—III

#### PLATE I.

Orientated from top to bottom roughly east to west. Typical Chiltern Ravine country with differences in elevation of 300 feet. The outcrop of the chalk rock, at the base of the upper chalk, is associated with the steepest slopes and stunted beech growth. The small crowns and the close canopy, due to the scarcity of merchantable trees, produce a characteristic effect on the photograph. The best example is situated on the southern side of the larch plantation, easily identified towards the bottom of the photograph by the cross rides and minute crowns. The larch extends along the summit of a spur, the narrowest point of which is just to the east of the plantation. Farther to the east the spur broadens out into a pear-shaped head, and its northern, eastern, and more especially its southern slopes are marked by stunted beech. At intervals along the southern slope, the early stages of "dying off" among the beech are featured by a greyish tint on the photograph reflecting the yellow leaves, attributable to the action of drought on the very shallow soil. Owing to the south-easterly dip of the strata, water seepage above the marl beds at the top of the Middle Chalk is pronounced along the lower southern slopes, and considerable windfall, coupled with fungal attack, is featured by the open stocking. Along this line ash regeneration is profuse. On the loam-with-flint soils in the valley bottom, still farther to the south (on the right-hand edge of the photograph) tall well-grown beech occur. Similar beech occur in the pear-shaped wood in the main valley to the north of Wormsley House. Apart from two small copses, the main valley to the south-east is all arable. The variations in the depth of loam-with-flint soils are clearly reflected by the crops. The grass in the Park, immediately to the north-east of the house, also reflects the soil differences. The rough grass on the chalk banks bordering the arable fields may be contrasted. The mixed vegetation to the south and west of the house consists of various tree species and shrubs, while in a secondary valley adjoining, to the north-west, a spruce plantation (centre of the photograph) can be distinguished by the small dark crowns of the trees. In another secondary valley farther to the north-west a similar spruce plantation can be identified. The beechwoods surrounding it on three sides include several types typically associated with different soils. But to appreciate fully these and other features shown by the photograph, it should be examined with overlapping prints in a stereoscope.

#### PLATE II.

Orientated from top to bottom roughly north-east to south-west. The escarpment marks the boundary between two major regional units—the Avon Vale to the west and the Wiltshire Downs to the east. The escarpment itself is a minor regional unit with very steep slopes, capped by the Lower Chalk on top of the Upper Greensand or Malmstone. Rough grass, thorn scrub, and woodland with ash and beech, are characteristic. Landslips have been a feature in the past and the easier slopes immediately to the west have in consequence a very



*Photographed by the Aircraft Operating Co., Ltd.*

No. 01714. Beechwood, Wormsley, England. Except in the immediate vicinity of the house and in the plantations, the forest is almost pure Beech. A little Oak occurs, particularly on the valley Loam-with-Flints; Ash is replacing the Beech where the latter is dying off. Scale: approx. 1/11,800.

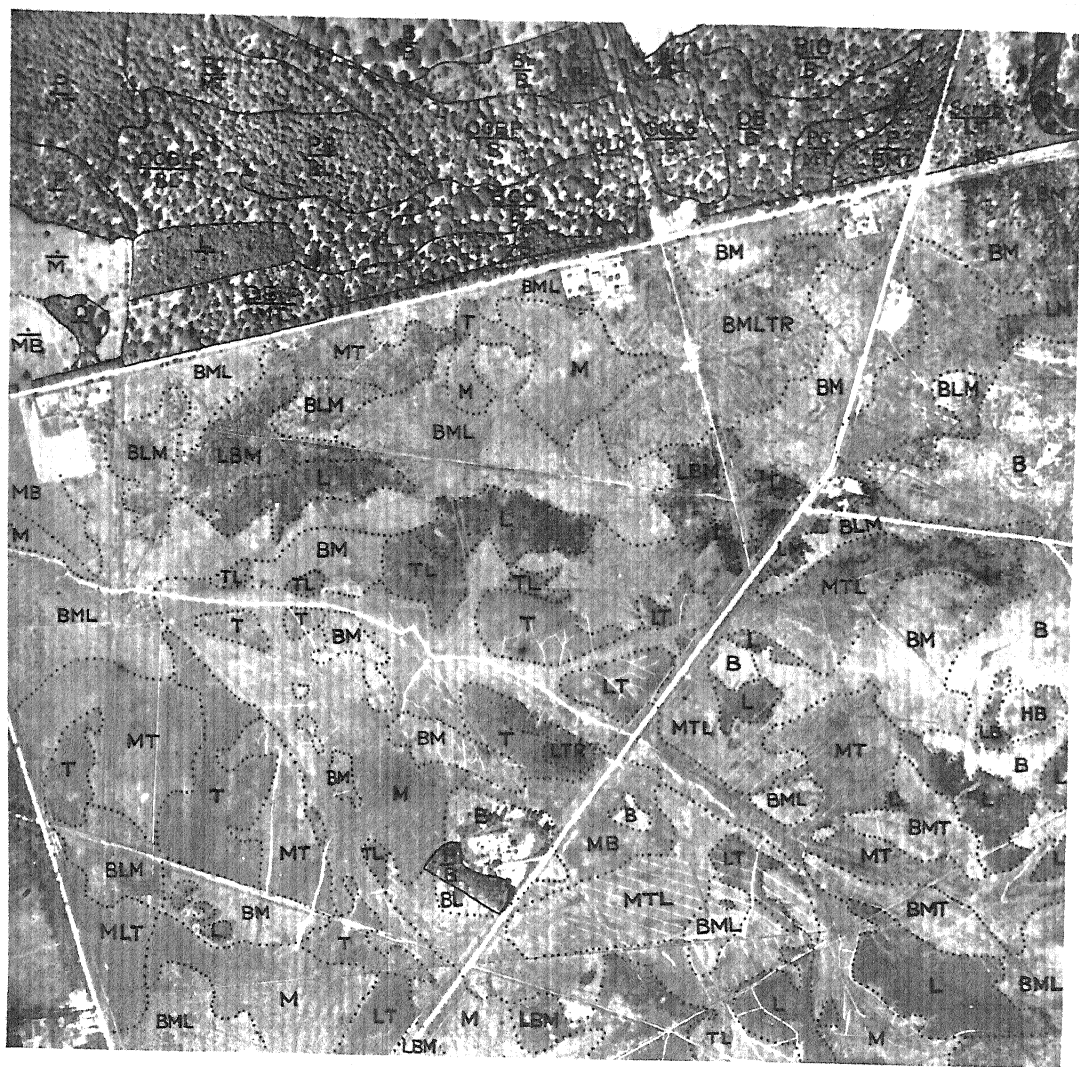




*Photographed by the Aircraft Operating Co., Ltd.*

No. 02432. Chalk escarpment S. of Highway, and 3 miles N.E. of Calne, Wiltshire, England.





Photographed by the Aircraft Operating Co., Ltd.

No. 01974. Crowthorne. Boundary of Forest Type: —. Boundary of Soil Flora: .....

Tree species: O = Oak; B = Beech; Bi = Birch; S = Spruce; C = Spanish Chestnut; L = Larch; P = Scotch Pine.

N.B. In the forest the principal tree species are shown over the line and the general soil flora type below.

Soil flora: B = Bracken; L = Ling (*Calluna vulgaris*); H = Heath (*Erica cinerea*); T = Bell Heather (*Erica tetralix*); M = *Molinia* and associated grasses; R = *Rubus* spp;

In a mixture the order in which the species are shown does not indicate so much their numerical frequency as their apparent dominance.

## ROBBINS—AN ECONOMIC ASPECT OF REGIONAL SURVEY

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irregular surface and variable soil, with the Gault Clay exposed beyond. The arable fields below the escarpment to the south-west mark the position of an exceptional slip and form a definite terrace. Below these fields and roughly parallel to the escarpment the irregular field boundaries mark the limit of the roughest ground. The fields above this sinuous boundary show signs of selective grazing by cattle and occasional indication of ancient cultivation. The fields below (left of the picture) all show half or three-quarter chain "ridge and furrow" lands, indicating that the soil wash over the Gault Clay automatically effected considerable drainage. But from the small size of the fields and the age of the elm trees, which are a feature of the hedge-rows on these lower slopes, it is probable that the majority were laid down to grass early in the last century. Turning to the Lower Chalk plateau (centre and right of the picture), which affords a striking contrast, the large open fields, all under arable cultivation, can be easily identified. With the exception of some accumulation of soil wash in a shallow depression at the head of the ravines to the south of the area, the soil is extraordinarily uniform. The effect on the crops of allowing wet farmyard manure to drain into the soil beneath the dumps, before it is spread out, is particularly marked on two plots. The intervals which have elapsed since some of the other plots have been manured can be roughly gauged by the prolonged effect.

#### PLATE III.

Orientated from top to bottom roughly north to south. Situated on the escarpment slope of the Barton Sand, Bracklesham Loam and Clay, and Bagshot Sand outcrops. The first, which are the highest beds, outcrop to the south-east in the right-hand bottom corner. The last only outcrops in the wood and is stocked mainly with oak, birch, and beech, with bracken dominant in the ground flora. The greater part of the area pictured is situated on the Bracklesham Loams and Clays, the loams being sandwiched between two plastic clay beds. Locally there are relics of Flint Gravel and down-wash of the Barton Pebble Bed and Sand. Wherever no great depth of gravel or sand lies over the Upper or Lower Bracklesham Clays, iron pans have formed over the clay. They may be of any age and may be classed as geological rather than pedological pans. The heath is in course of invasion by ling, which only occurs in its bushy form on two or three gravel caps. In this form the ling shows up dark in the photograph and probably marks the position of open gaps in the old Scots pine forest which was cut down during the war. In its creeping form the ling still shows up darker than the *Erica tetralix*, and in flower the two are very easily distinguished by colour when actually seen from the air. The distribution of *Erica tetralix* is mainly confined to the loams and clays, either pure or in mixture with *Molinia*, but extends also on to the iron pans. The most continuous area of iron pan is featured by the shallow parallel drains which show up white in the photograph. Of all the species in the ground flora, *Erica tetralix* alone is at all reliable as an indicator of soil conditions in this area. But even with this species the true nature and capacity of the soil may be obscured. In the woodland, where it occurs as a dominant in the ground flora on pans, loam, and clay soils, the differences in the soil are clearly marked by the tree species and their growth-form. On the clays oak and Spanish chestnut are common, and on the loams are associated with very good growth of Scots pine, but on the pans the pine is pure and stunted. These last features are not easily distinguished on the photograph, but using the latter as a map the various crops in the woodland and heath, covering in all about a square mile, were delimited and interpreted in four hours.

# THE VEGETATION OF THE LONGMYND

By W. LEACH.

(With Plates IV and V and three Figures in the Text.)

## INTRODUCTION.

SINCE the publication, some years ago, of a number of general accounts of the vegetation of various parts of the British Isles, primary survey work in this country appears to have fallen more and more into the background. This is not due to any depreciation in the importance of primary survey, but rather to the fact that the modern tendency is for the ecologist to concentrate on problems of a more intensive nature. The fact remains, however, that the recorded accounts of British vegetation are still far from complete, and consequently it would seem inadvisable that this branch of the subject should be entirely neglected and left in its present unfinished state. The urgency of the matter becomes more and more evident as we continually see fresh tracts of our more or less natural areas brought under the influence of modern developmental schemes.

The following is a brief account, in the nature of a reconnaissance, of the Longmynd area. This is a hill area of semi-natural vegetation some 8 miles long and 4 miles broad, and running roughly north and south near the western border of Shropshire (latitude  $52^{\circ} 30'$ ). The vegetation is uniform in general type with that of most of the lower hills of the Welsh border. It also possesses a number of features in common with the Heath Association of the eastern moorlands of Yorkshire (2).

## TOPOGRAPHY AND GEOLOGY.

The Longmynd is a plateau whose average altitude is between 1400 ft. (420 m.) and 1500 ft. (450 m.), while the highest point stands at 1696 ft. (509 m.) above sea level. The top in general has a gentle slope from west to east, with the result that the main drainage is towards the eastern side. That side of the hill is, in consequence, intersected by a number of deep stream valleys, some of which have almost cut back to the western edge of the plateau. On the western side the streams are smaller and much shorter, and their valleys are for the most part shallow.

Geologically, the Longmynd is composed of rocks of a markedly acidic nature. According to Blake (1) they fall into two groups, viz., the older eastern group or true *Longmyndian* which is predominantly grey in colour and consists of grey, green, or purple shales and slates interbedded with hard greywackes, and the younger western *Longmyndian* group, the rocks of which are predominantly red.

These latter consist of massive, but not very constant, beds of conglomerate with grit beds, and some subordinate slate (4). Blake (1) classes the grey series with the upper part of his Precambrian Monian System and the red with his "Lower Cambrian Series." The beds for the most part dip steeply in a westerly direction, in some places being practically vertical, and the rocks as a whole are not of a markedly porous nature.

#### THE CHIEF PLANT COMMUNITIES OF THE AREA.

Viewed in a broad way, the vegetation of the Longmynd area may be assigned to two well-marked plant associations, viz. oak forest and heath. The surrounding lowlands show ample indications of having originally supported forest of *Quercus robur* with the usual complicated accompaniment of hydrosere communities along the stream courses. *Q. robur* as a dominant gave place to *Q. sessiliflora* on the drier and shallower soils of the hill slopes, and woodland dominated by this latter species ascended to an altitude of from 1200 to 1400 ft. (360 m. to 420 m.). Above this level, it seems likely that the forest association gave place to the heath association, which was probably largely dominated, as it is now, by *Calluna*, and again relieved in its monotony by related hydrosere communities.

The lowland forest has, of course, now entirely disappeared, so far as its original form is concerned, and its site is occupied chiefly by grazing land. Occasional small woods occur, as will be seen on the map (Fig. 1); these are mostly of a mixed type, but they usually contain a number of pedunculate oaks. The original sessile-oakwoods of the slopes are all gone, but we still find numerous isolated trees of this species; also occasional plantations of a semi-natural type are to be found there. The slope vegetation, as it exists at the present day, is for the most part the result of tree felling and grazing by sheep and rabbits.

The summit heath seems to present the most natural appearance of any vegetation in the area, but even this, as will be seen later, must show features which differ considerably from those possessed in former days, as a result of its being now used as a grouse moor.

In this account the chief points of interest connected with the vegetation of the slopes, of the summit plateau, and of the stream courses will be dealt with. The lowlands do not present any relevant features of special ecological interest, and do not, strictly speaking, belong to the Longmynd; they will not, therefore, be considered further.

#### THE VEGETATION OF THE SLOPES.

The most characteristic feature of the slopes of the Longmynd is, almost everywhere, the presence of extensive stretches dominated almost entirely by bracken. Evidence that the greater part of this bracken-covered area was originally the site of a woodland is to be found in the presence of occasional

oaks (*Q. sessiliflora*), and of *Crataegus* scrub. In general, the scrub extends to a higher altitude than the oaks, a fact which suggests that originally it formed a zone along the upper limit of the oakwoods as is the case on the Pennines (6). These scrub communities are best seen in the long, deep, sheltered valleys on the eastern side of the hill (Pl. IV, Phot. 1). The vegetation of these easterly valleys presents, in the main, a very characteristic appearance. On the steep sides there is a ground flora largely composed of *Pteridium*, *Vaccinium myrtillus*, and *Festuca-Agrostis* turf. The *Pteridium* favours the sunny south-facing slopes, while the *Vaccinium* is most abundant or dominant on the north-facing slopes. Almost everywhere rabbit burrows are abundant and, where they are particularly numerous, a close *Festuca-Agrostis* turf, with or without an admixture of bracken fronds, usually surround the disturbed areas. Associated with this slope vegetation is usually a scrub composed chiefly of *Crataegus*, *Quercus sessiliflora*, *Sorbus aucuparia*, and *Ulex gallii*, with occasional trees of *Taxus baccata*. Where the sides of the valleys are very steep, denudation may be sufficiently active to bring about the formation of bare, scree-like stretches of rock fragments. These are usually found to be sparsely colonised by *Teucrium scorodonia*, *Pteridium*, or *Vaccinium myrtillus*, all of which are rhizomatous forms firmly anchored in the more stable subsoil. As we pass up these valleys the vegetation changes, more or less gradually, to that of the summit heath. The *Crataegus* scrub usually ascends right up to the head of the valley, disappearing at an altitude of round about 1200 ft. (360 m.).

The steeper western slope of the hill, with its poorly developed valleys, is exposed to the prevailing westerly and south-westerly winds. On this side trees are far less frequent, and mostly occur as isolated specimens scattered about the slopes, the most abundant being hawthorn, although a few oaks and rowans are also present. Almost everywhere along this slope we find bracken to be the dominant species. Bracken is, in fact, by far the most usual dominant on all parts of the Longmynd area which lie between altitudes of 900 ft. (270 m.) and 1250 ft. (375 m.). Below 900 ft. its spread is checked by farming operations, while above 1250 ft. it comes into serious competition with *Calluna*. As will be seen on the map (Fig. 1) it reaches its most extensive development at the north end of the hill, where it stretches right over Cothercott Hill, the highest point of which stands at 1457 ft. (437 m.).

Although definitely dominant, the bracken in the Longmynd area does not grow so tall and dense as to form the almost pure communities found in many other parts of Britain. There is always associated with it a greater or less admixture of typical grass-heath plants, such as *Festuca ovina*, *Agrostis vulgaris*, *Galium saxatile*, *Campanula rotundifolia*, *Potentilla erecta* and *Viola riviniana*, and the usual associated bryophytes of which the commonest are *Hypnum schreberi*, *H. cupressiforme*, *Hylocomium squarrosum* and *Dicranum scoparium*. In places the fern thins out and is replaced by patches of *Festuca-Agrostis* turf. This, as mentioned above, may occur owing to the presence of





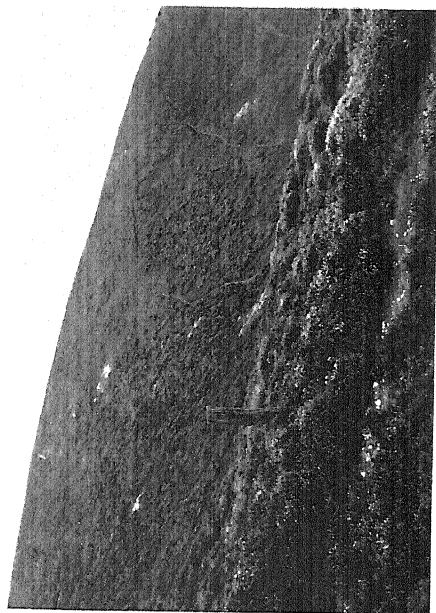
Phot. 2. Junction between grit and purple slate beds on western side of hill. *Calluna* is seen in abundance on the grit to the right of the picture.



Phot. 4. General view of valley A, in which the distribution of plant communities is shown in Fig. 3.



Phot. 1. View looking up Minton Batch showing *Crataegus* and *Q. sessiliflora* scrub. A yew is seen in the background on the left.



Phot. 3. Slope above valley marked A on Fig. 1, showing degenerating *Calluna*.

## LEACH—THE VEGETATION OF THE LONGMYND

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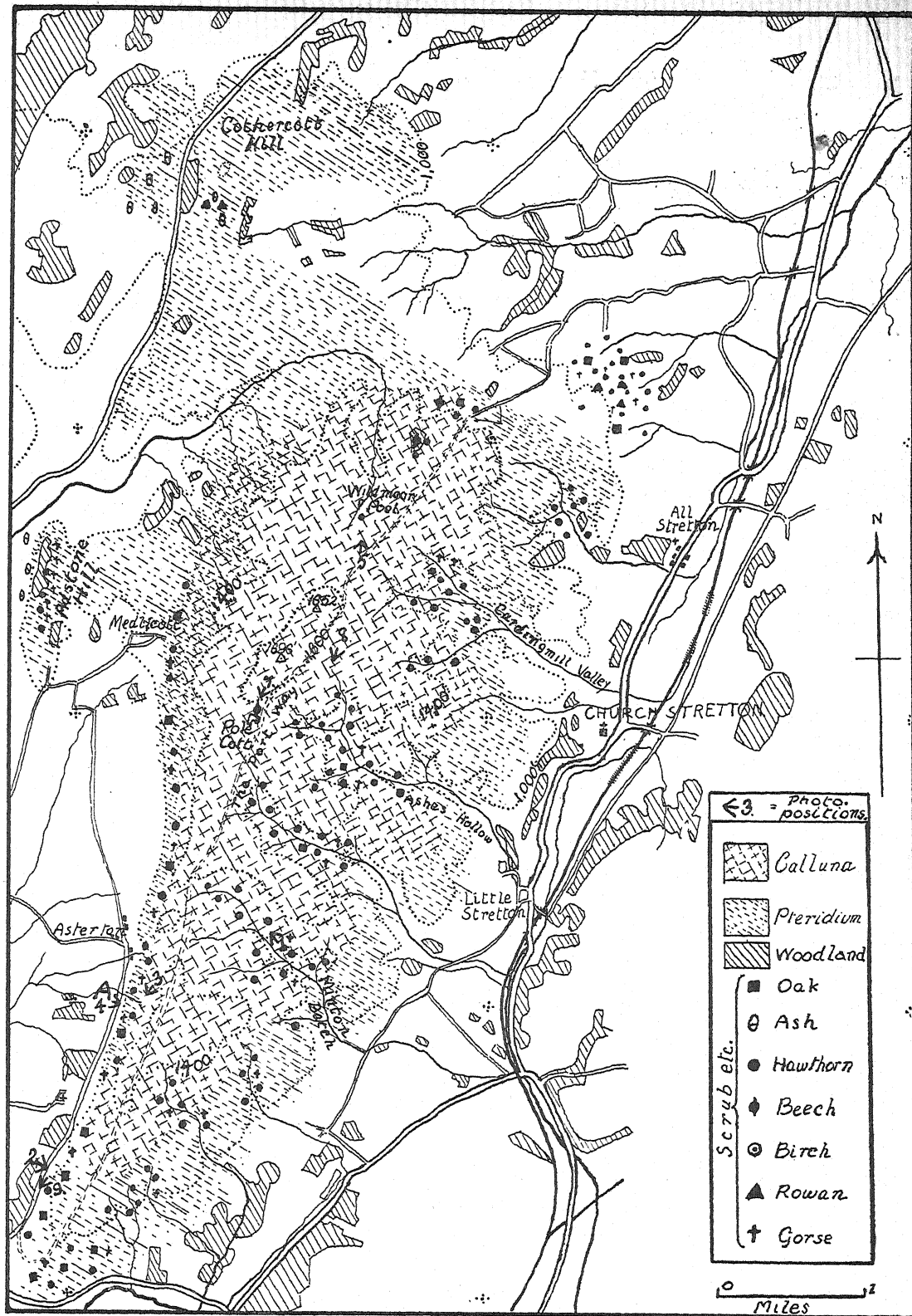


FIG. 1. Map of the Longmynd showing the more important features of the vegetation. The approximate positions from which the photographs illustrating this paper were taken, and their directions, are indicated by arrows and numbers.

rabbit burrows, but it may also be frequently traced to human agency. The fern is, in many parts, systematically cut and dried by farmers to form bedding for cattle. Incidentally this cutting tends to check the growth of the bracken and encourages the growth of the grasses, thereby increasing the grazing value of the land. On the other hand, there are frequent areas that at one time were pastures free from bracken, and are now, after a period of neglect, again becoming rapidly overgrown with fern.

Mention has already been made of the occurrence of *Ulex gallii*. This species almost invariably occurs associated with *Pteridium*, either as a subordinate species or as a dominant over small areas. Where such *Ulex*-dominated communities occur, they may, perhaps, best be considered as facies of the *Pteridietum*. The *Ulex* bushes are usually of the rounded-cushion form produced by sheep grazing. This species appears to be most abundant at altitudes between 1100 ft. (330 m.) and 1200 ft. (360 m.). It often happens that these *Ulex gallii* communities appear as definite zones as, for example, on Adstone Hill. This hill will be seen on the map as a small outlier to the west of Medlicott. On its summit, at the north end, there occurs a cap of *Ulex gallii* surrounded by the normal *Pteridietum* which clothes most of the rest of the hill. Although in the Longmynd area *U. gallii* reaches its greatest development in the upper regions of the *Pteridium* zone, it extends upwards as isolated bushes into the *Calluna* zone at 1400 ft. (420 m.) and higher. At this upper limit, however, it obviously suffers from exposure, and is decidedly stunted in its growth. Praeger (7) describes a very similar distribution for *U. gallii* in Ireland, except that there the *Calluna* zone apparently extends lower than it does on the Longmynd, with the result that *Ulex* is typically associated with *Calluna*.

A rather interesting variation in the general *Pteridium*-dominated character of the vegetation of the western slope, as a result of edaphic conditions, is to be seen at the southern end of this slope near Plowden. Here the rock is a moderately hard grit, which crops out to form small crags with associated small accumulations of talus. On, and at the foot of these crags, occasional trees of *Q. sessiliflora* occur (Fig. 2). In this region *Calluna* is frequent right down to the 900 ft. (270 m.) contour, and in places becomes dominant on the colonised talus slopes. *Pteridium* is also present in patches in varying abundance, but owing to the fact that the soil is often thin or absent, it is apparently unable to gain its usual ascendancy. The presence here of the *Calluna* seems quite definitely to be connected with the nature of the underlying rock. Proceeding along the hillside in a northerly direction, we pass from the grit outcrop on to the beds of purple slate. This change in the substratum is reflected in the vegetation, as we simultaneously pass from a region of conspicuous *Calluna* to one on which that species is absent, or only very occasional, so far as the lower slopes are concerned. Instead we find the characteristic *Pteridium* and *Festuca-Agrostis* communities (see Pl. IV, Phot. 2). The transition is quite abrupt, and takes place exactly along the junction between



the two types of rock. Upon what actual properties of the substratum this distribution of the plant communities depends, it is not easy to say. A point of some significance is the fact that the soil resulting from the weathering of the grit was found to be more acid than that produced by the weathering of the slate, the former having a  $pH$  4.2, and the latter  $pH$  5.9. From the above it rather seems as though, below 1200 ft. (360 m.), *Pteridium* owes its ascendancy over *Calluna* to edaphic factors, whereas on the top of the hill climatic factors are definitely responsible for the dominance of *Calluna*.

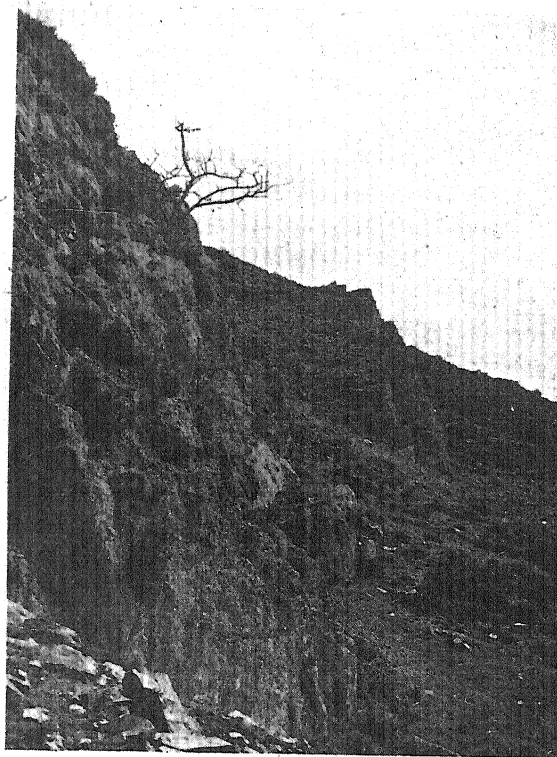


FIG. 2. View of western slope near southern end of the Longmynd. *Q. sessiliflora* and *Calluna* growing on rock (grit) exposure. *Calluna* on talus slopes. This photograph is indicated as 9 on Fig. 1.

The whole of this western slope is heavily grazed by sheep and, at the same time, rabbits are very numerous. The effects of this grazing are not obvious in the *Pteridium*-dominated parts; they are, however, clearly seen as we pass upwards to the region where *Calluna* becomes dominant. Here occurs the typical degeneration of the *Calluna* and its replacement by *Festuca-Agrostis* turf, a condition very similar to that described by Farrow (3) as being brought about by rabbits in Breckland. The net result of this grazing

factor in this transition region is that the *Calluna*, as a definite dominant, is, in most places, pushed back to a higher altitude than would otherwise be the case. Between the *Calluna* and the typical slope vegetation there is a transition zone in which various degrees of biotic degeneration of *Calluna* are present. In the lower parts of this zone the *Calluna* is largely replaced by *Festuca-Agrostis* turf, but higher up, close-cropped *Vaccinium myrtillus* may be dominant (see Pl. IV, Phot. 3).

A rather interesting phase of this transition region is to be found in the small valleys of the western slope. Fig. 3 shows a diagram, which is approximately to scale, on which is indicated the typical distribution of plant communities in one of these shallow valleys. The actual valley represented in the diagram is to be found on the map (Fig. 1) about three miles from the south end of the hill, and is marked A. It is also shown in Pl. IV, Phot. 4. The most striking feature of the vegetation of these valleys is the relative distribution of *Vaccinium myrtillus* and *Pteridium aquilinum* on the two opposite slopes. On the slope which faces north, a community dominated by closely grazed *Vaccinium* extends down to an altitude of about 1100 ft. (330 m.), whereas on the opposite side of the valley *Pteridium* is dominant right up to the *Calluna* region. This arrangement of these two communities is repeatedly to be met with in the small valleys of the western side, and can be recognised, though in a less marked degree, in some of the larger ones on the eastern side of the hill. It is interesting to find a similar distribution of *Vaccinium* and *Pteridium* described by Elgee as occurring on some hillsides in Yorkshire (2). Elgee puts forward the tentative suggestion that it is due to differences in the amount of exposure present on the two slopes. The occurrence of this similar state of affairs on the Longmynd strongly supports the exposure theory. The average temperature of the soil is lower on the north-facing slopes than on the south-facing slopes, a fact which becomes very obvious when one sees how much longer snow lies on the former than on the latter in early spring. A further interesting observation on the effect of exposure on the distribution of *Pteridium* is described by Praeger (7). On the hills south of Dublin he finds *Pteridium* occupying slopes facing east, and *Calluna* occupying corresponding slopes facing west. He attributes this distribution to the fact that the *Pteridium* prefers the slopes that are sheltered from the west winds, and in such positions is able to compete successfully with the *Calluna*. It seems likely that, here on the Longmynd, we have a somewhat similar case to that described by Praeger, except that the grazing factor is of sufficient importance to exclude the *Calluna* and bring about the dominance of *Vaccinium*.

#### SCREE VEGETATION.

The presence of screes on the slopes of the Longmynd has already been mentioned. They are nowhere of sufficient extent to warrant a lengthy treatment of their vegetation. Where they occur they are comparatively small,

and in many places they are fairly obviously of recent appearance, being formed by the erosion of slopes that were previously stable and covered with

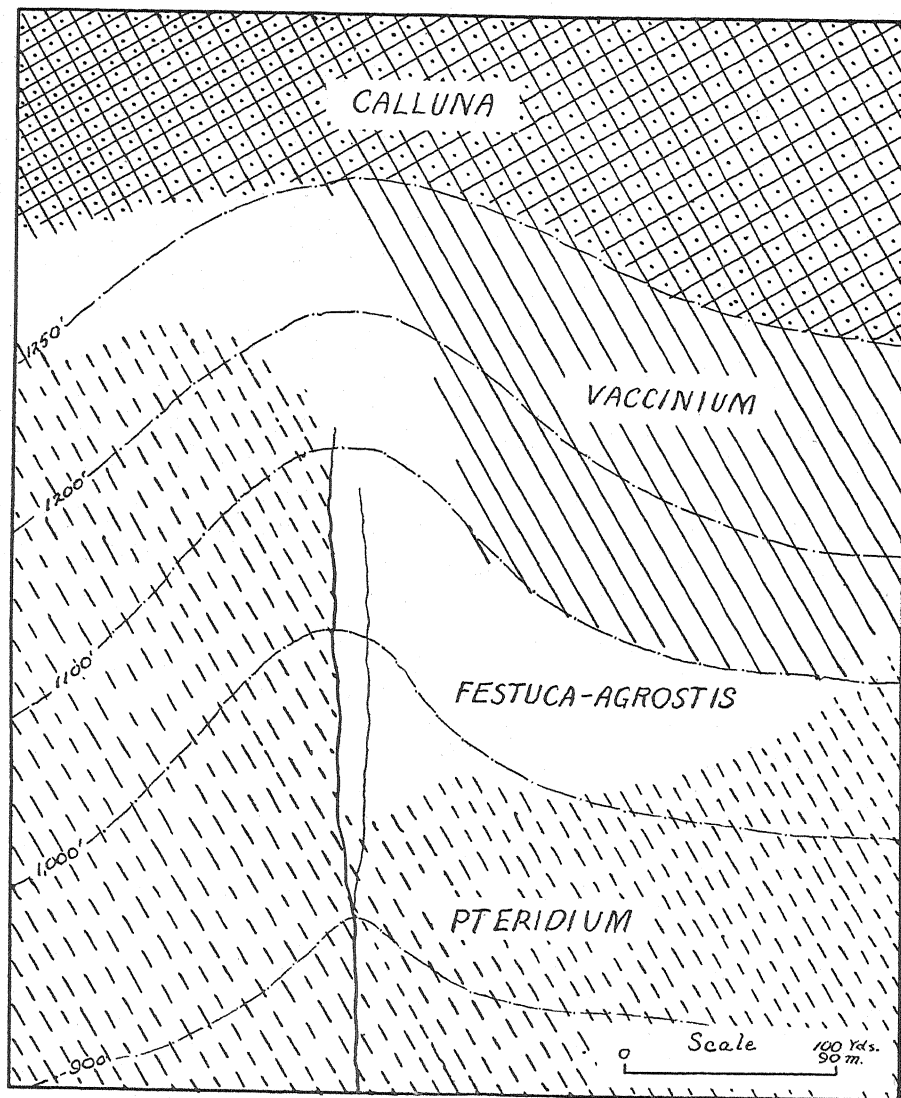


FIG. 3. Diagram indicating the approximate distribution of the chief plant communities in the valley marked A on Fig. 1. For further description see text.

vegetation. Frequent examples of recolonisation and stabilisation are to be met with, but the plants concerned in these processes are usually rhizomatous types such as *Pteridium*, *Teucrium scorodonia* and *Vaccinium myrtillus*. Occasionally the fern *Dryopteris filix-mas* occurs as a talus coloniser, but in general

it seems that here, owing to insufficiency of atmospheric humidity, the succession beginning with bryophytes and ferns is of rare occurrence (5).

#### THE VEGETATION OF THE SUMMIT PLATEAU.

Passing up the slopes between the altitudes of 1250 ft. (375 m.) and 1400 ft. (420 m.), we cross the already mentioned transition region in which *Calluna* makes its appearance, and often is dominant. In this zone, however, the *Pteridium*, *Festuca-Agrostis*, *Ulex*, and scrub communities occur, but only to a subordinate extent as compared to the heath vegetation dominated by *Calluna* and *Vaccinium myrtillus*. Above 1400 ft. (420 m.) is true *Calluna* heath. This summit heath forms a rather monotonous rolling landscape (see Pl. V, Phot. 5) over which *Calluna* is the chief dominant, although repeated firing by gamekeepers causes the vegetation to have a patchwork appearance. There are frequent patches in which *Pteridium* is present in varying abundance, from a sparse occurrence of isolated fronds to complete dominance. As a result of this periodic burning, all stages occur, often beginning with complete absence of visible living plants, and passing through dominance by *Vaccinium* to dominance by young *Calluna*, and finally to deep *Calluna*. It seems fairly obvious that the already mentioned areas which are dominated by *Pteridium* also owe their existence to burning, as where the fire has passed over a region where bracken is present as sparsely arranged fronds, a great increase in the abundance of this species always results.

The type of community that probably approaches the "climax" for the area is to be found in those places where burning has not recently taken place. Here the *Calluna* occurs as large, dense, somewhat straggling shrubs about 2 ft. high, the only constant associated flowering plants being *Vaccinium myrtillus* and *Deschampsia flexuosa*. Both of these latter are frequent in occurrence, and exist in a somewhat etiolated state in the shade of the *Calluna*. In addition to these there are occasional plants of *Lycopodium clavatum*, while covering the ground beneath the *Calluna* is a thick mat of *Hypnum cupressiforme* and *H. schreberi*. This moss carpet is, even in dry weather, usually quite moist, and must be an active agent in the formation of peat. Also it may account for the occasional appearance of *Pteridium* even in this deep *Calluna*, as, although no prothalli of the fern have so far been observed, it obviously provides suitable conditions for the occasional germination of spores of this species.

Two further species of occasional occurrence in this "climax" heath are *Ulex gallii* and seedlings of *Sorbus aucuparia*. The gorse appears to be growing here more or less under limiting conditions, seldom projecting many inches above the general level of the ling, and often forming spreading, flat-topped bushes which reach no higher than the "general vegetation level (8)." A noticeable effect of the prevailing westerly winds can be seen in the growth form of the *Calluna*, the stems of which are all more or less inclined towards





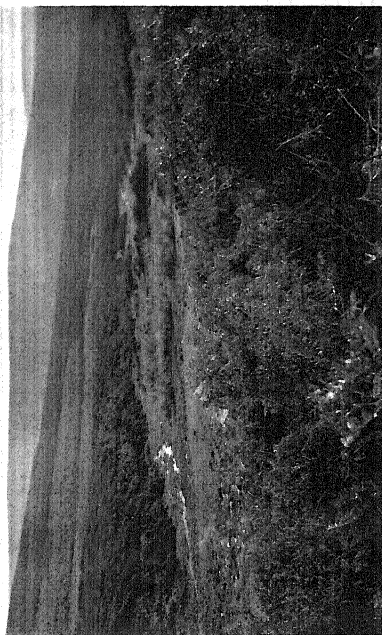
Phot. 5. General view of summit heath looking across Wildmoor Pool. Patchwork effect of burning is seen in the vegetation beyond the pool. Cothercott Hill is seen in the distance.



Phot. 6. View of *Calluna* and *Sorbus aucuparia* community on Stiperstones. For description see text.



Phot. 7. View of Pole Cottage showing trees and hedge of *Fagus*, and pasture land, in summit *Callunetum*.



Phot. 8. Stream and flush in the *Callunetum* above Ashes Hollow.

## LEACH—THE VEGETATION OF THE LONGMYND

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the east. This easterly trend is most strikingly seen on those areas where deep *Calluna* has just been burnt, leaving only a more or less parallel arrangement of charred main shoots, all running from west to east.

The question arises as to what would be the ultimate type of plant community to colonise this summit plateau if the burning factor were entirely removed. In connection with this problem the presence of the seedlings of the rowan may be considered. The repeated burning apparently never allows these young trees to grow beyond a height which is more than a few inches above the *Calluna*. The effect of arresting the action of the burning factor so as to allow a further development of the rowan can be seen on the Stiperstones, which form the next ridge of hills parallel to and to the west of the Longmynd. The summit of the Stiperstones, which stands at an altitude of about 1700 ft. (510 m.), bears a periodically fired *Calluna-Vaccinium* heath type of vegetation, very similar to that on the Longmynd. Near the highest point of the hill the vegetation is divided into more or less isolated strips by bare stretches of boulder detritus. These stretches of detritus have had the effect of isolating certain strips of vegetation from the fires that frequently occur. The result is that on these we find an open community of rowan trees with a ground flora dominated by *Calluna* (see Pl. V, Phot. 6). Whether, if left undisturbed, the rowan would become completely dominant and form a wood casting sufficient shade to change the dominance in the ground vegetation from *Calluna* to *Vaccinium myrtillus*, it is difficult to say. This is because no areas so far have been met with in which freedom from burning has persisted long enough to show the ultimate result. There seems to be sufficient evidence on the Longmynd to show that prolonged freedom from burning would probably, in many places, produce a similar rowan community to that on the Stiperstones. This tendency of the rowan to establish itself readily on these hills is probably connected with the fact that deep peat does not form on their summits, and that the bed rock is never far from the surface of the soil. Examinations of the peat thickness on the top of the Longmynd showed that it seldom if ever exceeds 1 ft., while on the deep *Calluna* areas the average depth is about 6 in. On those areas where signs of recent burning are evident, the peat thickness varies from 1 to 4 in.

A point of interest is the scarcity of birch trees in the Longmynd area. This species does not show the usual tendency to establish itself there, either on the site of previous oakwoods or on the summit heath. In fact, only one example of a birch tree has been seen by the writer on the top of the hill, and this stands all by itself near that artificial sheet of water known as Wildmoor Pool (see map, Fig. 1).

A species of tree which is able to exist reasonably well under the conditions prevailing on top of Longmynd is the beech. Of course it is a planted species, and is used to form hedges round a gamekeeper's cottage known as Pole Cottage, which stands at an altitude of 1570 ft. (471 m.) near the highest

point of the hill (see Pl. V, Phot. 7). A further point of interest shown by this photograph is the fact that it is possible to maintain reasonably good pasture land on this area which, if left alone, would pass over to heath, like that on the rest of the hilltop.

There is ample evidence to show that, even in prehistoric times, the top of Longmynd was the scene of human activities, as a considerable number of tumuli are present. How far this actually affected the vegetation in those days it is impossible to say. We, however, may reasonably conclude that, from very early times, occasional burning must have taken place. It is also significant that the ancient road, the Portway, runs along the top of the hill from end to end. This was doubtless for the purpose of keeping to the more open, and consequently safer, country of the plateau at a time when dense forest occupied all the surrounding lowlands.

#### STREAM-SIDE VEGETATION.

Mention has already been made regarding variation in the general character of the vegetation due to the presence of streams. This variation shows most conspicuously where it occurs on the *Calluna*-dominated parts of the hill top (see Pl. V, Phot. 8). On the lower slopes, where the stream-side vegetation is usually of the same colour as the surrounding plant communities, it does not produce so striking a contrast.

The streams running down the sides of the hill do not, in their upper courses, cut channels which are much below the general level. The result is that there is on either side nearly always a wet zone of a width which varies with the gradient of the stream course. The soil of these zones naturally shows a gradual increase in water content as the bank of the stream is approached, which results in a corresponding graduation in the plant species which cover it.

Usually, whether the stream is traversing the summit callunetum or the communities of the slopes, the outer limit of the wet zone is indicated by the presence of a *Festuca-Agrostis* turf with a greater or less admixture of *Nardus stricta*. As the stream is approached and the soil water content increases, the *Nardus* becomes more abundant, and is associated with other moisture-loving species. These form a mixed community with no well-marked dominant, of which a typical composition is given below:

<i>Nardus stricta</i> L.	...	...	f.-a.	<i>Prunella vulgaris</i> L.	...	o.-f.
<i>Carex flava</i> L.	...	...	f.-a.	<i>Ranunculus flammula</i> L.	...	o.-f.
<i>C. diversicolor</i> Crantz.	...	...	f.-a.	<i>Lotus corniculatus</i> L.	...	o.-f.
<i>Anagallis tenella</i> Murr.	...	...	f.-a.	<i>Cnicus palustris</i> Willd.	...	o.
<i>Juncus bulbosus</i> L.	...	...	f.-a.	<i>Drosera rotundifolia</i> L.	...	lf.
<i>Hydrocotyle vulgaris</i> L.	...	...	f.	<i>Mentha aquatica</i> L.	...	f. along edge of water
<i>Myosotis caespitosa</i> Schultz.	...	...	o.			
<i>Triglochin palustris</i> L.	...	...	r.	<i>Apium nodiflorum</i> Reichl.	f.	in water

In addition to these flowering plants, mosses form a conspicuous component of the community. The most abundant of these are *Philonotis fontana*, *Hypnum cuspidatum*, *H. revolvens*, *H. falcatum*, *H. vernicosum*, and *Aulacomnium*



*palustre*. *Philonotis*, owing to its pale yellow-green colour, is very conspicuous, and it frequently forms almost pure fringes to the banks of the streams.

The streams mostly originate from springs situated near the top of the hill. Those which give rise to the streams flowing west are actually on the summit plateau, and are surrounded by well marked boggy flush areas. The point where the spring emerges is usually marked by a dense growth of *Sphagnum squarrosum* Pers. var., *subsquarrosum* Russ., *Dicranella squarrosa* and *Polytrichum commune*. In the centre of this moss area there is very often a small pool in which *Potamogeton polygonifolius* Pourr. grows. This species also extends into the moss area, where it produces upright aerial leaves. Surrounding these flushes is a zone of the *Agrostis-Nardus-Carex* turf similar to that which borders the stream courses lower down. A point of some interest is that *Lotus corniculatus* frequently grows in abundance on the *Sphagnum*. Immediately below one of these springs it is typical to find a broad wet flush area dominated by *Juncus effusus* and bearing also most of the above listed stream-side species. This gradually tails off as the water collects together to form a definite stream.

In conclusion, I wish to thank the University of Birmingham Joint Standing Committee for Research for a grant towards the expenses incurred in the course of this survey, and Dr P. G. M. Rhodes for help in the identification of some of the mosses.

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## ON THE PEAT DEPOSITS OF MOINE MHOR

By CHARLES G. C. CHESTERS.

(*With eight Figures in the Text.*)

MUCH detailed research has been carried out on the identification of remains discovered in post- and inter-Glacial peat deposits in the British Isles, Europe and North America, and a large amount of data has accumulated with regard to the correlation of these remains. Attempts have also been made to trace the development of woodlands from the fossilised pollen of the peat. The general condition of the vegetation during the periods which lie between the end of the Glacial time and the end of the Sub-Atlantic time (5) has often been discussed, but so far no very detailed and systematic investigations have been made on the succession of vegetation which developed on the surface of the several raised beaches which occur round the western sea-board of Britain.

This paper records the results of a general investigation of the various peat strata formed on the surface of the 50-ft. raised beach which surrounds the head of Loch Crinan, in Argyllshire, and underlies the moorland of Moine Mhor (Fig. 1). A salt marsh has developed on the shoreward side of the present beach, and a gradual transition occurs between the salt marsh vegetation and the vegetation of the moorland, so that an investigation of the lower layers of the peat resting on the surface of the raised beach might yield evidences of any former salt marsh vegetation which was formed on the surface of that older beach.

Davis (3) has studied the peat underlying salt marshes at Boston and has shown that, where the peat contains salt marsh plant remains, the species present are those that grow near high-tide mark at the present time.

It is possible that the surface of the raised beach might have been invaded directly by a type of moorland or a scrub vegetation, and it has been recorded by Lewis (6) that birch, hazel and alder remains were found covering the surface of the 25-ft. raised beach in the case of the Moss of Cree (lying between Newton Stewart and Wigtown). These were followed, in the higher layers, by *Sphagnum*, *Eriophorum* and *Phragmites*. From evidence furnished by a study of other peat mosses he suggests that: "Interest should attach to an examination of any deep peat deposits resting on the 50-ft. raised beach—as we might expect to find in that case—the representatives of the Arctic Zone of the Merrick Mosses resting on the surface of the beach."

Erdtman (4) has described a peat moss occurring "at the 50-ft. raised beach," about 14 m. above sea level, and north-west of the upper end of Loch

Carron (Ross-shire). Pollen of *Alnus* and *Betula* was found throughout all the strata, and in larger quantity than pollen of *Pinus*. Pollen of *Corylus*, *Ulmus*

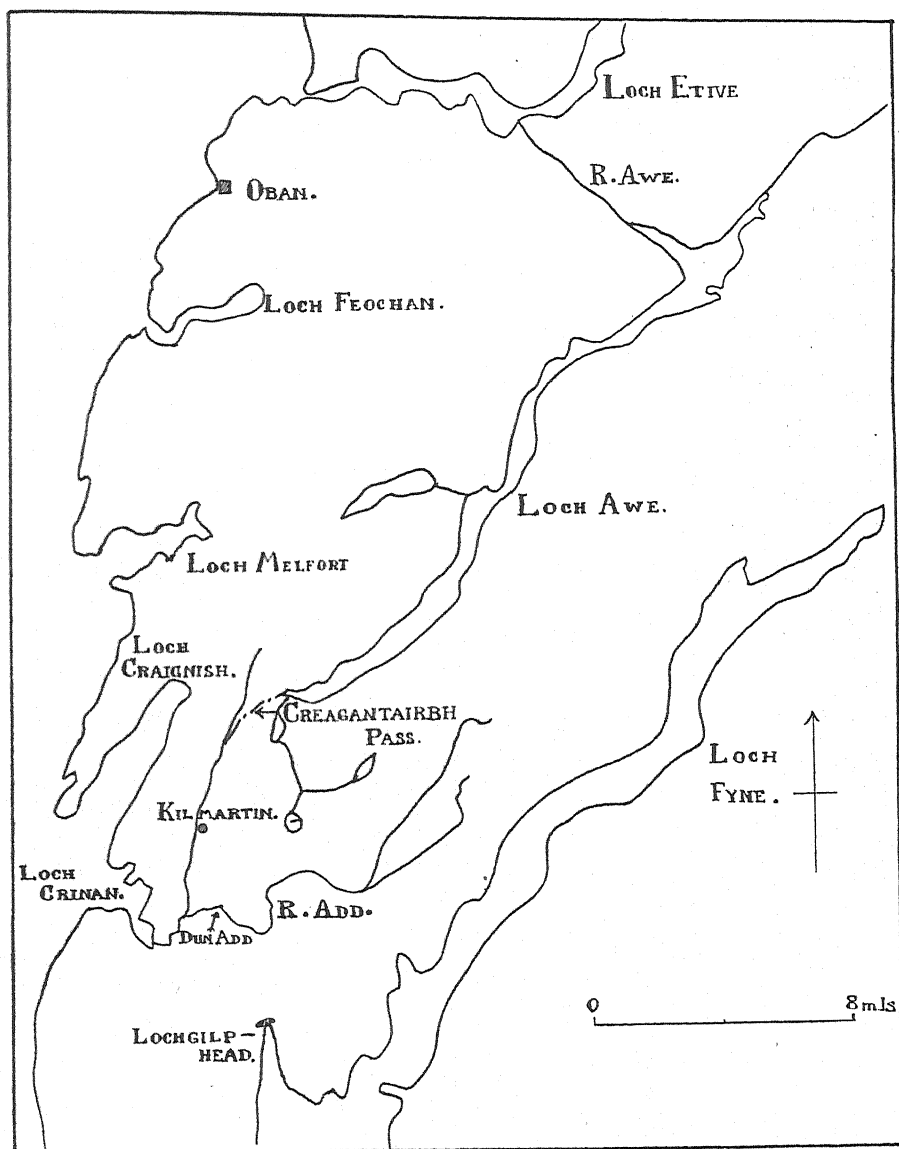


FIG. 1. Map of Northern Argyllshire showing the region surrounding Loch Crinan and the approximate position of the former exit of Loch Awe, during Glacial times, via the Creagantairbh Pass. (Based on the  $\frac{1}{4}$  in. to the mile Geographical Survey map.)

and *Quercus* was less frequent, and was not represented in all the layers. The high frequency of *Alnus* pollen is outstanding in this moss.

Before beginning the description of the plant remains of the peat, it will be of interest to consider briefly the topography and the geological history of the area here under consideration.

Loch Crinan, one of the sea lochs of Argyllshire (Fig. 1), is surrounded by the wide tract of moorland known locally as Moine Mhor, or the Crinan Moss. At one time the whole region, including the Moss, was one large, almost land-locked sea, into which flowed a river now represented by the River Add. The

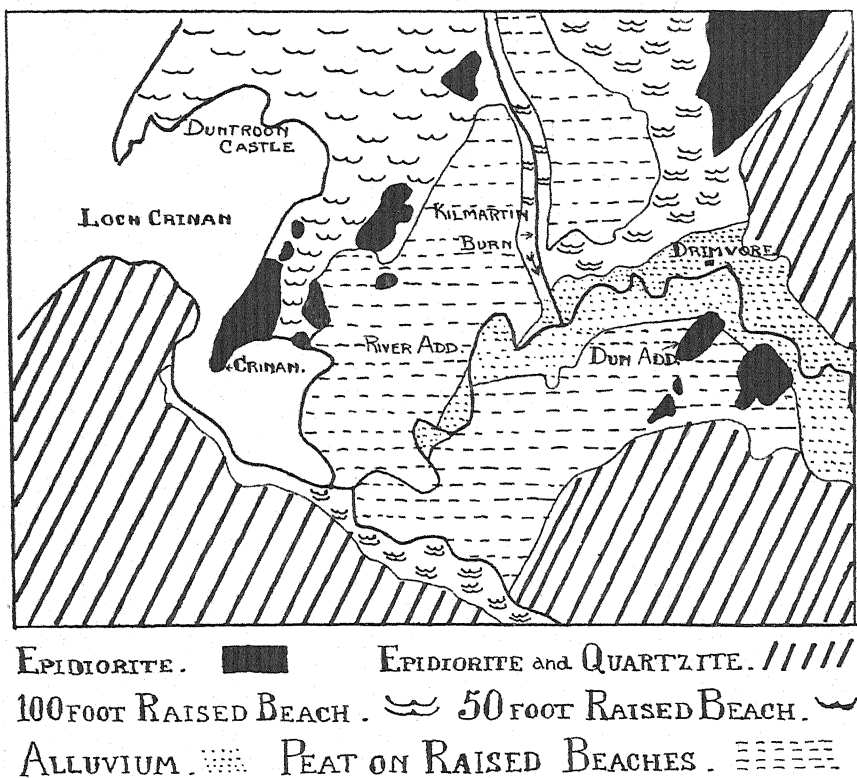


FIG. 2. Geological drift-map of Moine Mhor and the Kilmartin Valley. (Based on the  $\frac{1}{2}$  in. to the mile Geological Survey map.)

promontory on which stands the old village of Crinan (Fig. 3), and the many mounds of epidiorite schist which rise from the surface of the Moss, are the remnants of islands of that ancient sea (Fig. 2). The flat expanse of Moine Mhor breaks the series of hill ranges which are characteristic of this part of Argyllshire, and separates the highlands of North Knapdale from those of more northern Argyll.

At present the River Add alone serves to carry the drainage water of these Argyllshire hills to the sea, but in late Glacial times the overflow water of Loch Awe escaped over the watershed into the Add, due to the damming

back of its former exit by ice. At a later date, when the ice had somewhat retreated, the drainage water of the Loch escaped through the Creagantairbh Pass (Fig. 1) into the Kilmartin Valley, and, via the course of the present Kilmartin Burn, joined the River Add (7). Aided by these two distinct streams at different periods, the Add appears to have silted up the higher

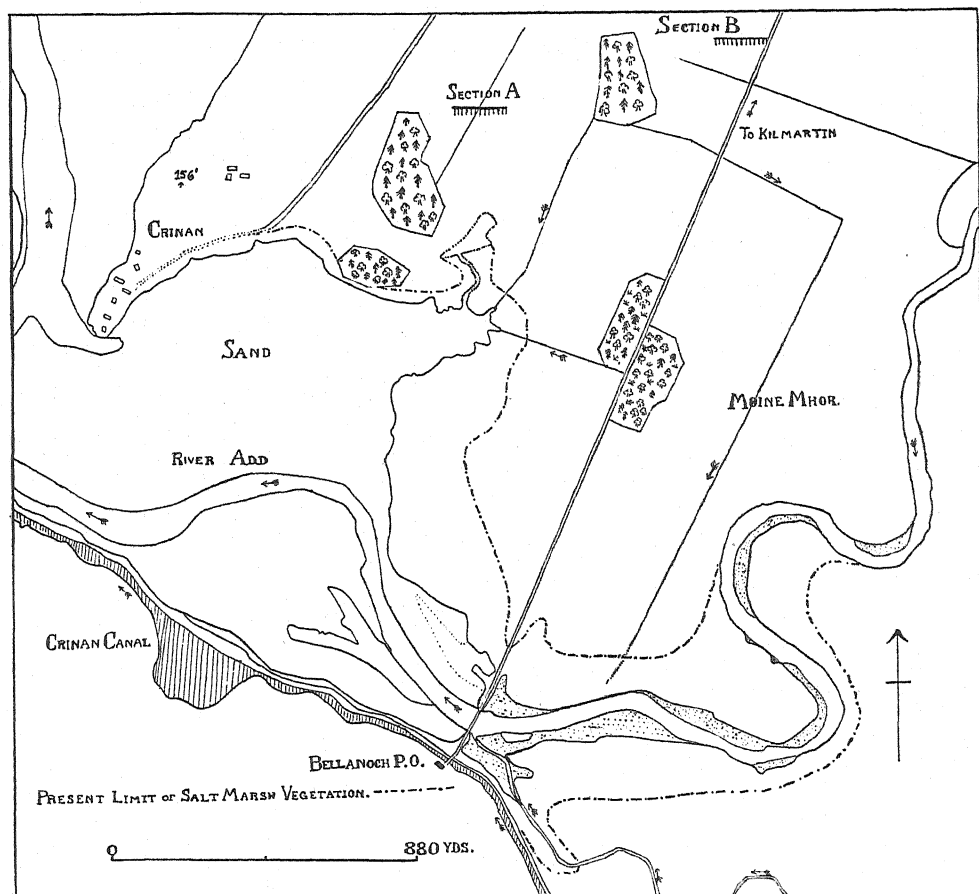


FIG. 3. Map of the estuary of the River Add indicating the position of the peat sections examined and the approximate limit of salt marsh vegetation at the present time. (Based on the 6 in. to the mile Geographical Survey map.)

portion of the inland sea. Later, the general rise of the west coast of Scotland caused the formation of the 100-ft. beach, which passes round the head of Moine Mhor and extends upwards into the Kilmartin Valley (Fig. 2). A further uplift formed the 50-ft. beach on which the peat of the lower, or seaward part, of Moine Mhor has been deposited (Fig. 2). Along the course of the Add the 50-ft. beach is masked by several river terraces and alluvial deposits, but, along the Bellanoch-Kilmartin road, the transition from fine sand on the



seaward side of the moor to coarse sand and gravel near the village of Kilmartin, can be followed in the various sections which have been cut for the excavation of peat fuel.

Boulder clay occurs below the 50-ft. raised beach and outcrops between tide levels in a bay south of Duntroon Castle (Fig. 2). In this blue-grey clay thirty-three species of Mollusca have been identified by Crosskey and Robertson (2) many of which are Arctic or Boreal forms. Its presence below the 50-ft. beach of Moine Mhor is suggested by numerous exposures along the course of the River Add; a particularly good section, near the farm of Drimvore (Fig. 2), shows 10 ft. of horizontally bedded gravel resting on stiff grey boulder clay.

There is a dominance of *Nardus stricta* and *Scirpus caespitosa* in the vegetation of the central portion of the moor, and they are accompanied by *Erica cinerea*, *E. tetralix*, *Calluna vulgaris*, *Molinia caerulea* and various species of *Juncus*; *Juncus squarrosus* covering large tracts of wet, low-lying ground, where it is mainly associated with *Sphagnum* sp. On the western and eastern edge of the moor, and also along the higher reaches of the Add, *Myrica gale* dominates the vegetation and is mainly associated with *Calluna* and *Erica tetralix*.

The outcrops of epidiorite schist—with the single exception of Dun Add, an old Scottish fortress—are covered by woodland in which the dominant tree is *Pinus sylvestris*, but in some cases *Picea* also occurs, along with *Betula*, *Fraxinus* and *Corylus* (Fig. 3). The last species is more common in the woods near the sea. It is doubtful whether or not these woods are natural, and local tradition speaks of the pines, at least, having been planted. Along the Bellanoch-Kilmartin road two areas of woodland occur on the surface of the moor, and consist of a mixed *Betula* and *Alnus* scrub with a very few trees of *Pinus sylvestris* (Fig. 3).

Table I.

Layer	Character of peat of Section A	Depth of layer	
		inches	cm.
8	Present subsoil ... ..	1	2.5
7	Dark brown peat of open and coarse texture ... ..	8	20.0
6	Dark brown peat of close texture with a band of light brown moss peat $\frac{1}{2}$ in. (1.8 cm.) deep in the centre ... ..	6	15.0
5	Light brown peat of open texture ... ..	4	10.0
4	Brown peat of close texture ... ..	10	25.0
3	Dark brown peat of very close texture ... ..	18	45.0
2	Fine black peat ... ..	4	10.0
1	Fine silver sand representing the surface of the 50-ft. raised beach ... ..	—	—
	Total depth ... ..	51	127.5

The peat examined was collected from two sections used for cutting peats, the one, lying E.N.E. of the old village of Crinan behind one of the wooded

mounds; the other, about  $1\frac{1}{2}$  miles N.N.E. of Bellanoch. The sections are marked A and B respectively (Fig. 3), and the depth and character of the several layers present is given in Tables I and II.

Table II.

Layer	Character of peat of Section B	Depth of layer	
		inches	cm.
8	Present subsoil ... ..	1	2.5
7	Dark brown gritty peat ... ..	3	7.5
6	Dark brown granular peat with a layer of grit separating it from 7 ... ..	11	27.5
5	Very light brown spongy peat ... ..	2	5.0
4	Light brown peat consisting of an upper layer of open texture and a lower layer of close texture ... ..	12	30.0
3	Dark brown peat, the upper layers being laminated ... ..	18	45.0
2	Hard black peat containing 23 per cent. of fine sand ... ..	9	22.5
1	Coarse sand and gravel with worn pebbles—representing the top of the 50-ft. raised beach ... ..	—	—
	Total depth ... ..	56	140.0

Representative portions of each layer in the two sections, including the surface of the raised beach, were cut from fresh surfaces of the peat. Half of each portion was macerated in 40 per cent. NaOH for 6 hours. The material was then filtered through a perforated porcelain filter, and the filtrate centrifuged and examined for pollen grains. The larger remains were extracted from the solid material on the filter by soaking it in a large volume of water.

Table III.

Layer	Section A	Section B
7	Hypnum cupressiforme	Hypnum Schreberi
6	H. cupressiforme H. Schreberi	H. cupressiforme H. Schreberi Dicranum scoparium
5	H. Schreberi Hylocomium squarrosum	Sphagnum cymbifolium Hylocomium loreum
4	Sphagnum cymbifolium Dicranella heteromalla	<i>Upper layer</i> Sphagnum fimbriatum S. cymbifolium Dicranella heteromalla Aulacomnium palustre Hylocomium squarrosum <i>Lower layer</i> Dicranella heteromalla Hylocomium loreum Hypnum Schreberi H. cupressiforme
3	Hypnum Schreberi H. cupressiforme Plagiothecium denticulatum Aulacomnium palustre	None
2 and 1	None	None

Mosses play an important part in the constitution of the peat of both sections, but they occur at a lower level in Section A than in Section B.

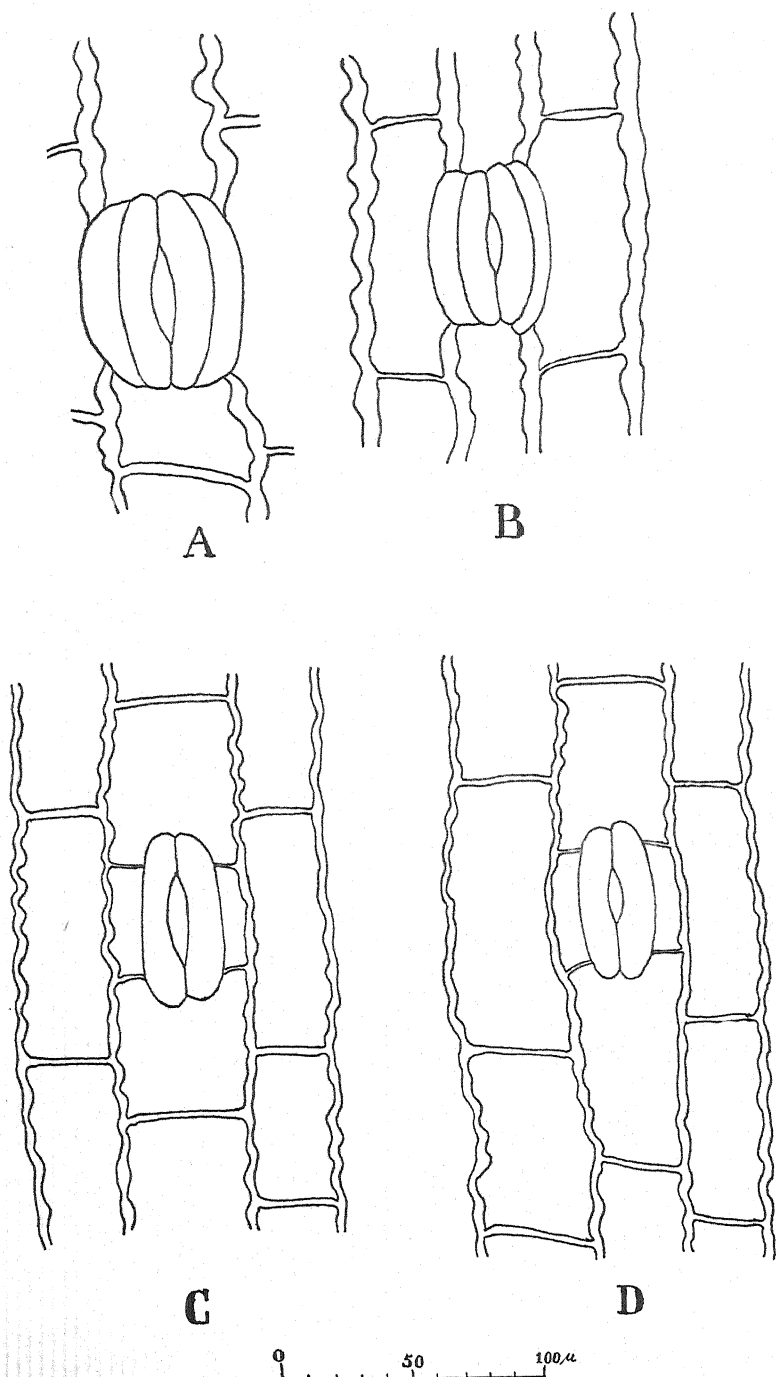


FIG. 4. Camera lucida drawings of stomata of *Eriophorum* and *Carex* from living material and material preserved in peat. A. Stoma of *Eriophorum vaginatum*. B. Stoma of *Eriophorum* sp. from peat. C. Stoma of *Carex binervis*. D. Stoma of *Carex* sp. from peat.



*Sphagnum* spp. were present in almost every layer along with other mosses, but they are only recorded from those layers in which both leaves and stems

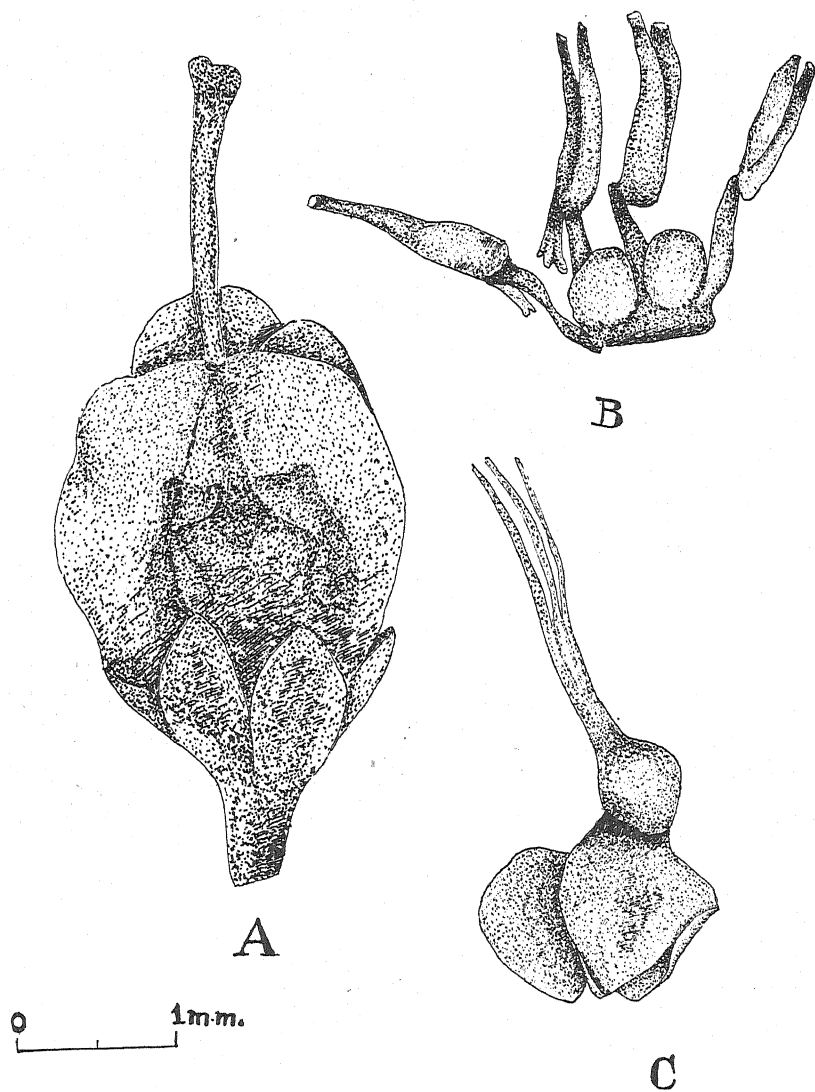


FIG. 5. A. Flower of *Calluna*. B. Anthers of *Calluna*. C. Fruit of *Carex* sp.  
Isolated from peat.

were present, or fragments of complete plants occurred. All the mosses were identified by, and classified in accordance with H. M. Dixon's *Student's Handbook of British Mosses* (3rd edition). The mosses present in the various layers are indicated in Table III.

All the species isolated are characteristic of either a moorland or woodland vegetation of the present time. No clearly marked succession is evident, as, for example, from Arctic to more temperate types, or from mosses characteristic of damp situations to those of drier. Local variations, such as may be encountered in any woodland or moorland, appear to be indicated by the occurrence of *Aulacomnium palustre*, which would indicate a damper situation, but there appears no striking variation or interruption of their occurrence such as might be expected if a gradual transition from one type of vegetation to another had occurred.

Few of the phanerogamic remains were in a high state of preservation either in the natural peat or in the material left after maceration, and those portions extracted were mainly parts of stem, bark, leaves, leaf "cuticles," flowers and fruits. The leaves and flowers were most perfectly preserved, and

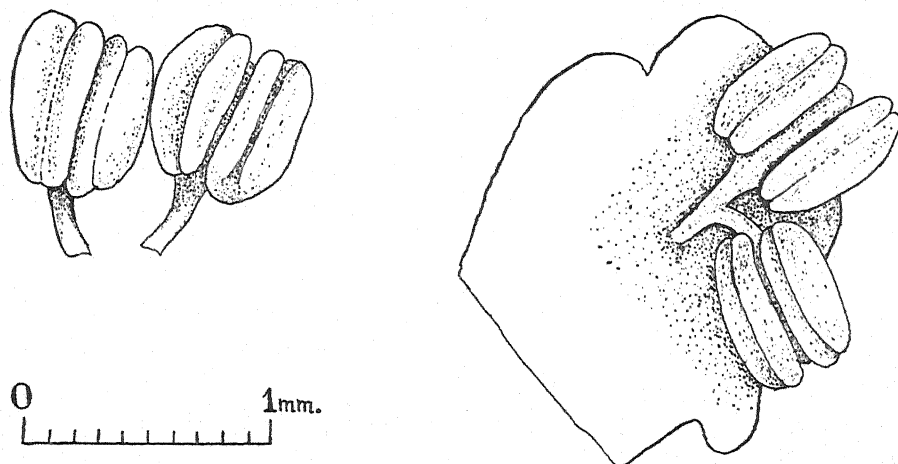


FIG. 6. Separate anthers, and stamen attached to bract, of *Betula* isolated from peat.

in some cases were easily identified. The majority of the remains belonged either to the Ericaceae, *Betula* or *Myrica*. Numerous graminaceous cuticles were encountered, and after comparison with living types, as suggested by Bandulska (1) in the case of the Fagaceae, it was possible to distinguish *Carex*, *Eriophorum* and *Juncus* cuticles from those of the true grasses (Fig. 4). Several flowers of *Calluna* and isolated anthers of that species (Figs. 5, A, B), a group of anthers of *Betula* (Fig. 6), and a single *Carex* fruit (Fig. 5 C) were obtained. A grass panicle, resembling an opened panicle of *Festuca*, was recovered from one of the higher layers. A systematic table of these remains from the two sections is given in Tables IV and V.

The results stated lead to the conclusion that any succession of vegetation which has occurred represents the gradual encroachment of a moorland type of vegetation on a birch heath. Remains of birch trunks have been noted in the lower layers of other sections than the two described at about the surface

of the raised beach, and for some 3 ft. above the beach surface. In the material examined, many badly decomposed remains of stems, whose bark resembled that of *Betula*, were dug from layers 3 and 4; but only in the case of layer 3 of Section A was it possible to compare the wood under the microscope with that of present-day birch wood, when it was evident that the preserved wood belonged to the same species.

From the evidence of the moss flora and that of the higher plant remains, the assumption seems justified that Moine Mhor has, from very early times, been covered with a type of vegetation which is essentially similar to that of any present lowland moor. The earlier layers appear to suggest that the moorland was slowly encroaching upon a birch heath in which clumps of trees were separated by areas of *Calluna*, more or less extensive. Damper periods must have existed during the succession, as is suggested by the presence of mosses such as *Sphagnum* and *Aulacomnium*, and by the presence of *Erica tetralix*, *Juncus* sp. and *Myrica*.

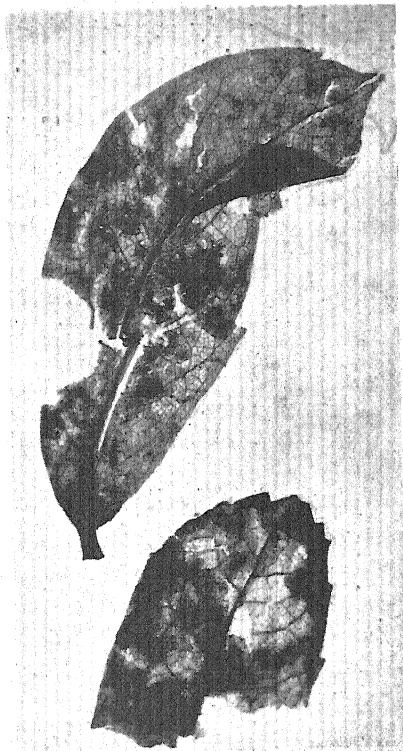


FIG. 7. Photograph of leaves of *Myrica* from peat. Note the characteristic serration of the apex of the lower leaf.

Table IV. Section A.

Layer	Specimens identified
7	Leaves of <i>Eriophorum</i> , <i>Juncus</i> and <i>Myrica</i>
6	Stems of <i>Calluna</i> . One fruit of <i>Carex</i> (sp.?). Leaves of <i>Eriophorum</i> and <i>Myrica</i> , and scale leaves of <i>Juncus</i>
5	Stems of <i>Myrica</i> . <i>Carex</i> stomata
4	Stems of <i>Erica tetralix</i> . Leaves of <i>Erica tetralix</i> , <i>Carex</i> and <i>Juncus</i> (spp.). Flowers of <i>Calluna</i>
3	Stems of <i>Betula</i> and <i>Calluna</i> . Leaves of <i>Myrica</i> (Fig. 7). Remains of leaves and stems of <i>Juncus</i> (sp.) and a grass. Stamens and bract of <i>Betula</i>
2	<i>Juncus</i> (sp.) stem and basal leaves
1	Sand of "raised beach"

There is no positive indication that the surface of the raised beach has ever been covered by salt marsh vegetation, but it appears probable that the more central region of the Moine Mhor remained in a marshy condition in its

early stages of development, as is suggested by the high percentage of sand in layer 2 of Section B. The presence of a considerable amount of chitinous material strongly suggests that aquatic animals of some type lived in the immediate vicinity of this layer.

Table V. Section B.

Layer	Specimens identified
7	Remains of epidermis of <i>Juncus</i> (sp.). Grass panicle resembling <i>Festuca</i>
6	Stems of <i>Calluna</i> . Leaves of <i>Juncus</i> (sp.)
5	Decomposed remains of leaves represented only by their vascular skeleton
4	Terminal portions of stems of <i>Calluna</i> . Stems and attached leaves of <i>Erica tetralix</i> . Leaves and stems of <i>Myrica</i> . Abundant flowers of <i>Calluna</i> . Leaves and basal portions of stems of <i>Juncus</i> . Remains of a grass cuticle
3	Bark resembling that of <i>Betula</i> . Remains of Gramineous cuticle
2	Remains badly preserved—no clear structural features observed
1	Sand with considerable amounts of chitinous material

Study of the fossil pollen of the several layers of the two sections confirms, in a general way, the evidence derived from the phanerogamic remains. Pollen grains of *Betula* occur in almost every layer of the two sections and, in a large majority, pollen of the Ericaceae was found in considerable quantities; spores of *Sphagnum* (sp.) and pollen of grasses were less frequent. The number of pollen grains of *Alnus* and *Corylus* varied somewhat but never reached any large value (Fig. 8).

Preparations examined by Dr G. Erdtman, to whose kind assistance I am deeply indebted for the results stated, give an idea of the character of the pollen content of both sections. These preparations were made from material from Section B, and in layer 2 the following figures were obtained:

33	pollen grains of <i>Betula</i>
19	" " <i>Alnus</i>
4	" " <i>Corylus</i>
2	" " <i>Ulmus</i>
1	" grain of <i>Ilex</i>
	Tetrads of the Ericaceae
	Pollen grains of Compositae and grasses
	Spores of <i>Sphagnum</i> (sp.)

A preparation made from the material of layer 3 yielded:

40	pollen grains of <i>Betula</i>
3	" " <i>Alnus</i>
2	" " <i>Quercus</i>
3	" " <i>Corylus</i>
1	" grain of <i>Pinus</i>
1	" " <i>Ulmus</i>
1	" " <i>Carpinus</i> (doubtful)
1	" " an Umbelliferae
1	" " a Caryophyllaceae
	Tetrads of the Ericaceae
	Pollen grains of grasses

In layer 7 the following were obtained:

27 pollen grains of *Betula*  
 3 " " *Corylus*  
 1 " grain of *Pinus*  
 1 " " *Alnus*  
 1 " " *Salix*  
 Tetrads of the Ericaceae  
 Spores of *Sphagnum* (sp.)

These results add confirmation to the view expressed above, that the early vegetation on the surface of the 50-ft. raised beach must have resembled a birch heath, and that during the succession which followed a gradual change

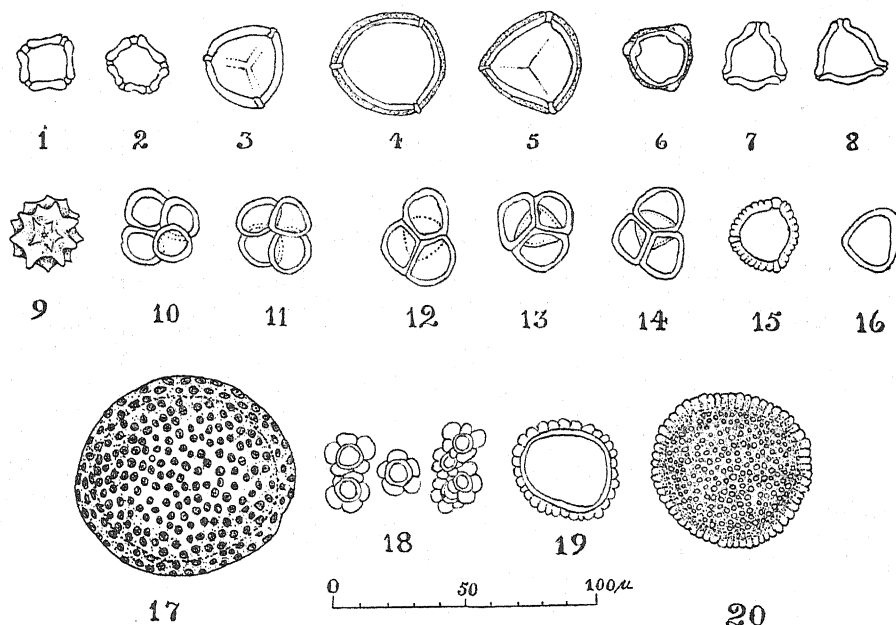


FIG. 8. Camera lucida drawings of pollen grains and animal remains from peat. 1, 2. Pollen of *Alnus*. 3, 4, 5, 6. Spores of *Sphagnum* (sp.). 7, 8. Pollen of *Betula*. 9. Pollen of a Composite. 10-14. Tetrads of the Ericaceae. 15. Pollen of *Salix* (?). 16-20. Animal remains.

to a purely moorland type occurred. This may in part have been due to a slight climatic change, as vegetation of a birch heath type is still found on the sides of the foothills surrounding Moine Mhor, but at several feet above its surface. Even if it were suggested that transference of pollen by wind from surrounding wooded areas might account for some of the pollen grains found in the peat strata, it is impossible that this should have any very serious influence on the results, and when the pollen statistics are coupled with the occurrence of macroscopic remains, more or less conclusive evidence of a wider extension of *Betula* than at present is indicated.

The investigation of two sections in such an extensive area of moorland cannot be said to yield, in any way, conclusive evidence of the history of the



moor, but, from the results, as far as they go, there appears to be no evidence of the existence of a former salt marsh vegetation on the surface of the raised beach. Exactly the contrary is indicated, that woodland, or at least a birch heath with numerous areas of *Betula* and other trees, was established at an early date. Again, the evidence does not support the view expressed by Lewis (6), that representatives of an Arctic flora should be found on the surface of the 50-ft. raised beach.

All the results suggest a close comparison between the succession of vegetation over the surface of the 50-ft. raised beach of Moine Mhor and that over the 50-ft. raised beach north-west of the upper end of Loch Carron, as recorded by Erdtman (4), but without the markedly high frequency of alder pollen.

The peat deposits over the raised beach at Crinan appear to be of recent origin. This is indicated by the presence of *Alnus* pollen, and by the almost entire absence of *Pinus* pollen. *Alnus*, according to the researches of Erdtman, was a late immigrant into Scotland, and its appearance in the peat of Moine Mhor would suggest that all of the peat was Post-Boreal. Between early Post-Boreal times and the present a definite maximum of *Pinus* pollen occurred, in Scotland, in Sub-Boreal times. The very low frequency of *Pinus* pollen, in the layers where it does occur, and its entire absence in others, would suggest that the peat of Moine Mhor was formed at some time after the *Pinus* maximum in Sub-Boreal times. It is probable that almost all, if not all, the peat of Moine Mhor has been deposited between the commencement of Sub-Atlantic times and the present day.

Deposition of peat is still going on, and in some of the oldest trenches used for "peat cutting," fresh layers of very recent origin, containing remains of *Eriophorum* and *Erica tetralix*, have been formed over the surface of the old workings.

It may be concluded, then, that in the area of Moine Mhor which is covered by the present investigations, there is no evidence either of the occurrence of salt marsh vegetation on the surface of the 50-ft. raised beach, or of the presence of any Arctic flora. The remains which have been examined are all those of typical moorland or woodland plants, and from the pollen statistics, taken in conjunction with the other results, it is suggested that the peat is of recent origin, the earliest layers probably dating back to Sub-Atlantic times.

In conclusion I desire to express my thanks to Mr W. Leach for his help and criticism during the preparation of this paper.

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# OBSERVATIONS ON THE DOMINANCE OF PTERIDOPHYTES ON SOME ST LUCIA SOILS

By C. W. WARDLAW.

(With Plates VI and VII.)

## I. INTRODUCTION.

THE island of St Lucia, B.W.I. (latitude  $14^{\circ}$  N.) is volcanic and mountainous, and supports in the interior areas of tropical rain forest. From time to time these virgin forests have been cleared for peasant "gardens" and more recently for banana plantations under conditions that inevitably lead to soil deterioration (4, 5). After a few years, crop production, in the absence of adequate soil conservation, falls off; the land is then completely abandoned and is quickly invaded by a rampant secondary flora. Under the humid conditions prevailing in the mountain gullies and ravines it has been observed that various Pteridophytes become dominant members of the new plant communities established on the abandoned areas. In this paper a brief account will be given of the changes that have led to this interesting situation.

## II. VIRGIN FOREST LAND.

In St Lucia the rain forest region consists of broken mountainous country with steep hillsides and deep ravines, well watered by a rainfall of 100 in. or more per annum. The areas to be discussed, at an elevation of some 400 ft., have a temperature range of  $62^{\circ}$ – $88^{\circ}$  F. (3). The virgin forest soils vary according to position and the exposure of the land, but fundamentally they are formed by the weathering and accumulation of volcanic materials derived from the original igneous agglomerates, tufas, breccias and grits (1). According to the type of weathering these soft volcanic rocks give rise *in situ* to red or yellow loam-like clay soils, which are further modified by the amount of organic matter present. Where the virgin forest remains intact the soils are found to be relatively good, being weathered out to a depth of 20–24 in. and well provided with organic matter in the top 12 in. The fertility of such soils may be attributed to a number of causes, including (a) the profound influence exercised by long accumulations and reactions of organic matter, (b) the deep weathering of surface rock materials by sub-aerial denudation and root activity, (c) the preservation of the surface soil once it has been built up, by the dense forest canopy, and (d) the long cycle of biological activities in which essential minerals are brought up from below and returned to the soil surface by leaf fall and the decay of twigs, trunks, flowers and fruits (6).

The vegetation of the area under discussion is of the tropical rain forest







Phot. 1. Forest of young *Cyathea* and *Cecropia* with a few banana plants still struggling in its midst. The banana plantation was abandoned in 1926 and the photograph taken in 1929.

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Phot. 2. Banana overtopped by *Cyathea*, with *Cecropia* beginning to form an overhead canopy.



Phot. 3. *Gleichenia* sp., *Lycopodium cernuum* and seedlings of *Miconia* sp. occupying the side of a road-cutting of slightly weathered rock in the banana country of St Lucia.

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type, and consists of a considerable variety of moderately tall trees covered with lianes, climbers, and epiphytes, with a scanty ground vegetation of Pteridophytes, seedlings and occasional bushes and Palms. The general forest canopy is provided by solitary specimens of *Mimusops globosa* (Balata), *Hymenaea courbaril*, *Inga laurina*, *Andira inermis* and *Richeria* sp., here and there penetrated by the loftier trunks of *Slonea* sp., *Nectandra* sp. and *Bursera simaruba*.

Towards the end of 1922 a considerable area of this virgin forest land was opened up for large-scale banana growing. The trees were felled and the logs allowed to rot. The herbaceous ground vegetation was burnt or cutlassed and the area was planted with bananas. By the end of 1926 the promoting company had become bankrupt and the plantations were abandoned. In the meantime, high precipitation, rapid and extensive soil erosion and depletion of organic matter, coupled with the lack of any adequate system of conservation, led to marked soil deterioration. Thus the original fertile forest was, in a relatively short time, replaced by a soil greatly inferior in all respects. In short, in such rough and broken country, where even the best soils are not of the first order of fertility, soil deterioration, in the absence of suitable methods of conservation proceeds rapidly, and in the brief space of five years a well-marked series of changes may take place.

### III. THE ESTABLISHMENT OF A SECONDARY FLORA.

When the writer first visited St Lucia in 1928, the banana lands had been abandoned for two years. During that time a secondary flora, quite distinct in character from the original primary forest, had invaded the plantations and was in open competition with the Gros Michel banana for the land. The banana, which requires good conditions to flourish, was reduced in stature and rate of growth as the result of the degraded condition of the soil and was quickly being outstripped by a rampant "weed" population less exacting in its requirements. The dominant members of this new flora which had made its appearance were *Cyathea* sp. (probably *C. caribea*), *Cecropia palmata* (trumpet tree) and *Sciadophyllum* sp. (an Araliad), among those with tree-like habit, and species of *Miconia* and *Peperomia* among the bush forms. Together with the remaining Gros Michel banana plants these constituted a dense impassable vegetation on the steep hillsides where originally orderly plantations had been established. In 1928 the tree ferns were more or less of equal stature with the bananas while *Cecropia* and *Sciadophyllum* rose a few feet above the general level of the vegetation. In 1929 the two latter species had grown, in some areas, almost to tree-like stature, while the tree-ferns were beginning to overtop the bananas (Pls. VI and VII, Photos. 1 and 2). On some hillsides the spreading banana foliage was still relatively conspicuous, but elsewhere it had been overgrown and obliterated and the plants were slowly becoming attenuated as the overhead canopy of secondary vegetation increased.



## IV. FERN SPECIES AS DOMINANT MEMBERS OF A PLANT COMMUNITY.

From a study of these derelict banana lands and of peasant "gardens" abandoned for 20 or more years (after a process of soil degradation comparable to that of the banana plantations), it has been conclusively demonstrated that reversion to the original forest condition does not take place, and that the invading secondary bush remains established for a very considerable period of time. This is in keeping with other similar records quoted by Warming (7).

The most significant and interesting feature of the secondary flora is the dominant position occupied by tree ferns, *Cyathea* spp., in the new community. From the agricultural point of view the composition of the invading weed population is undoubtedly indicative of soil of indifferent quality. The secondary flora flourishes because it consists of plants characteristic of waste places and not exacting in their soil requirements. By extending these observations it was found that the invading weed population included species which are the first to populate slightly weathered rock surfaces, land-slide areas, highly eroded open hillsides, and road cuttings. Thus the rock faces exposed by the deep road cuttings in St Lucia are, in the humid inland regions, populated entirely by species of *Gleichenia* and *Lygodium*, and *Lycopodium cernuum*. Pl. VII, Phot. 3, shows such a road cutting, of slightly weathered rock, in the banana country, populated entirely by *Gleichenia* sp., *Lycopodium cernuum* and seedlings of *Miconia*. In the same way *Cyathea* was found growing on weathered rock surfaces laid bare by land slides, and also on roadside cuttings. Given the necessary humidity the ferns therefore rank among the first colonisers of land where a true soil stratum has not been created. On this subject Treub (2) observed that three years after the eruption of Krakatau, when an entirely new land surface had been formed as the result of volcanic activities, the new flora consisted almost entirely of ferns. An investigation carried out in St Lucia on the rooting habit of *Cyathea* showed that the roots were spreading rather than deeply penetrating and that they appeared to be able to derive an adequate supply of the essential minerals from a partially weathered rock soil, poor in organic matter, in which rock fragments could still be observed. On these steep hillsides, where erosion has removed all the friable humus-containing soil, the materials of which the new land surface is composed are not greatly removed from the underlying parent volcanic rock. The success of the ferns in competing with their more highly equipped Angiosperm rivals is to be attributed, then, to their adaptability to growth on poor soils and to the humid conditions which permit of their life cycle being carried through. The peopling of a new area by a particular species depends on an ample output of spores or seeds, a means of dispersal, and suitable conditions for germination and growth. That the fern species are highly adapted physiologically to compete on this basis is proved by the important part they have

played in the population of abandoned cultivated lands and on rock soils exposed by cuttings and land slides.

With regard to the prevalence of ferns in the West Indies, Warming (7) observes: "On several of the more raised West Indian islands, for instance on Jamaica, which is extraordinarily rich in ferns, one finds on the mountains at a certain altitude, namely, in the cloud belt, a vegetation that may be termed fern-forest and includes such forms as *Cyathea* and *Alsophila*; this possibly gives us a blurred picture of one of the most ancient types of vegetation." In the virgin forests adjacent to the abandoned banana lands in St Lucia, the distribution of tree ferns would be more correctly described as *occasional* rather than as *abundant*. When a reproductive frond of species such as *Cyathea tenera* or *C. Caribea* reaches maturity, however, the number of spores liberated is enormous, while the distribution of plants over the abandoned areas testifies to the success with which the spores are dispersed. Given the amply moist conditions which prevail in the ravines and steep hillsides, young plants are successfully established in large numbers. By reason of the impoverished condition of the soil, actively growing competitors, whose luxuriant growth might otherwise smother the young plants, are eliminated, so that *Cyathea*, with its modest requirements and a root system physiologically adaptable, is enabled to take a prominent place among other plants in the repopulation of the abandoned areas.

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# THE BIRD POPULATION OF A SETTLED VALLEY IN THE WEST USAMBARAS, TANGANYIKA TERRITORY

By R. E. AND W. M. MOREAU.

## INTRODUCTORY.

AFTER our ornithological work had been confined for more than twelve months to the unusually interesting, but correspondingly difficult, evergreen rain forest round Amani, in the East Usambaras, the openness of the mountain country between Lushoto and Sakkarani, in the West Usambaras, came as a welcome change. Over an area approximately 15 miles in diameter the forest, which is said to have been continuous throughout the whole mountain-mass within living memory, has been cleared so completely that in a wide perspective it is frequently impossible to point to a single surviving tree. Large candelabra Euphorbias are a striking feature of the landscape. The annual rainfall has been reduced to less than 50 inches, and most of the cleared ground is devoid of permanent cover of any description. Once the gorge by which the mountains are entered from Mombo has been climbed, cultivation, apparently in annual alternations of crop and fallow, is practically continuous except where the hillsides break into cliffs. In most of the valleys there are permanent trickles of water a few inches or feet wide. Channels are led off from them to provide a certain amount of primitive irrigation. Where they are left to themselves and there is no pronounced gradient, these little streams carry a heavy growth of flowering rush (*Cyperus*). Not infrequently narrow strips of bush, approximating to hedgerows, line the paths.

Finding ourselves settled for a part of September 1929 in a valley about 8 miles from Lushoto, we were encouraged by the natural conditions to think that it might be possible not only to work out the species of birds inhabiting the valley, but also to form a trustworthy estimate of the number of individuals of each species. This paper deals with our results.

## TOPOGRAPHICAL.

The Kongei Valley is roughly in the shape of a bowl tilted down towards the south, with its lowest point about 4000 feet above sea-level. The soil varies in colour from brightest red through a variety of reds and browns to almost black in the most heavily cultivated land. The milkiess of the streams probably indicates a whitish clay subsoil in places. Outcropping rock appears to be gneiss.

The chief natural entrance of the valley is at the lowest point, by a bottle-neck between slopes about 100 feet high. These rise as they open out till, on

the north, their tops are at least 700 feet above Kongei, with patches of vertical cliff. Two European farms, about 25 years old, are situated in the valley. Together they occupy roughly a circular area of about 300 acres, the boundary of which runs along the top of the valley wall where it is lowest and maintains approximately the same level throughout its circumference. A little stream between steep banks bisects the valley and swampy patches occur elsewhere. The plant communities in the Kongei Valley differ markedly from those of the surrounding country and they are described in detail in a later section.

For our purpose the boundary of the combined farms was conveniently distinctive and also formed quite a good natural boundary. Where it did not run along the crest of a ridge, it was clearly marked by a native path and bordered on the outside by native cultivation. Whatever they may be at other seasons, these shambas, where the mealies had just been reaped or the ground hoed up in preparation for the next crop, were comparatively thinly populated with birds. The area of the farms formed, therefore, a well-defined natural unit. There was, however, one objection to the retention of the farm boundary as our boundary, namely, that part of it was lined with a row of trees. As E. M. Nicholson has pointed out, anything like a hedge, so far from acting as a natural boundary in respect of birds, presents itself to them as a highway and a base of operations.

#### METHODS.

We are aware that the most satisfactory season at which to determine the number of birds "carried" by any given area is when breeding is at its height, and the birds are in consequence more definitely localised than at any other time. We were not free agents in our choice of the date to visit Kongei, but it is doubtful if in any case we could have chosen a much better period of the year. Field work of any description is next to impossible in the "rains." Of East Africa as a whole it has been stated that breeding seasons generally are dependent on the "rains," but they are much less defined than in the Temperate Zones. In the Usambaras the greater part of the annual rainfall is recorded in two periods, between the end of March and the beginning of June, and between the end of October and the end of November. At Kongei in September an appreciable proportion of the birds were engaged in some phase of breeding activity. The loud song and pugnacity connected in the Temperate Zone with territory holding were little in evidence however, and we have yet to gain a clear idea of what part this element of bird-behaviour plays among tropical birds.

Having approximately fixed the "local habitations" of the more sedentary species, our plan of work was to divide the area into segments and work each segment on different days and at different times of the day, counting the numbers of each species seen. The average of the numbers so recorded should

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give a fair approximation to the regular population of each segment; and the total of the segments a good idea of the population of the whole valley.

In one respect we have failed; for the bush areas we can give no figures that are worth putting down. Such birds as *Prinias* and *Cisticolas* are so fugitive that several observers working simultaneously would be needed to give good results. It was possible to walk through a patch on one occasion without raising a twitter or a wing; and on another the place would be embarrassingly full of small and restless life. The small area of impenetrable "Closed Bush" remained an imperfectly known country to the end of our stay, as regards even the species it harboured.

### TYPES OF VEGETATION.

At the time of our census the area of 300 acres was occupied by the types detailed below, approximately in the proportions indicated.

*Type 1.* Grassland, 150 acres.

Resembling mountain grassland and composed of a pure stand of perennial grasses kept closely cropped by farm stock. Weeds or the flowering heads of grasses were entirely absent, except where this grassland merged on its borders into *Type 3a*.

One part of this area was sparsely dotted with small acacia trees, indicating vestiges of a parkland formation.

*Type 2.* The area that had been subjected to European cultivation subdivided as follows:

*Type 2a.* Areas planted with trees, 2 acres.

*Grevillea robusta* and *Eucalyptus* had been planted as shelter belts, and round the farms there were small orchards of peaches and oranges and a single clump of bamboos. In addition, there was a patch of neglected black wattle, *Acacia decurrens*, and along a mile and three-quarters of road *Casuarina* and *Grevillea robusta* (in flower) formed avenues in a single row on either side.

*Type 2b.* Market-garden crops, 24 acres.

Highly cultivated ground carrying vegetables and potatoes, devoid of trees.

*Type 2c.* Freshly ploughed land, 25 acres.

*Type 2d.* Cereals, consisting of maize recently harvested, 20 acres, and barley and rye, nearly ripe, 10 acres.

*Type 3.* Bush formation, apparently consequent on the influence of man. It is divisible into the following:

*Type 3a.* An open bush formation (50 acres) in a transient stage, composed of suffrutescent herbs up to 3 or 4 feet high, and confined to the steeper slopes towards the rim of the area studied. The grassland (*Type 1*) tended to merge into it. It had apparently established itself on land that had been under

cultivation during the last few years. The characteristic plants of this type were:

Shrubs: *Rumex maderensis* Lowe ("Sorrel"); *Cassia didymobotrya* Fres.

Suffrutescent herbs: *Solanum panduræforme* Drege; *Abutilon indicum* Don.; *Artemisia afra* Jacq. ("Wormwood"); *Psiadia arabica* Jaub.; *Vernonia iodocalyx* O. Hoffm.

Herbs: *Kalanchoë lanceolata* Pers. ("Life Plant"); *Aspilia abyssinica* Oliv. and Hiern.; *Ethulia conyzoides* L. (a characteristic weed in certain cultivated areas); *Rhamphicarpa tuberosa* Benth. (a semi-parasitic plant on the roots of grasses).

*Type 3b.* Closed bush formation in a sub-climax stage, composed of shrubs up to 7 feet high and covering an area of 2 acres on a very steep slope. It was understood not to have been disturbed for at least 20 years. The border of this type and the grassland was clean-cut; and *3b* nowhere came into direct contact with or merged into *Type 3a*.

*Type 4.* A swamp formation in which the dominant plant was a 6-8 feet tall *Cyperus* occurring in the stream bed and in isolated patches elsewhere.

*Type 5.* Fringing vegetation, open bush, similar in composition to *Type 3a*, and a few trees, none of great height, clothed the rough and steep banks of the rill bisecting the grassland (*Type 1*) for about 300 yards. It was only a few feet wide.

For identifications of the plants and for assistance in describing the above types we are much indebted to Mr P. J. Greenway, Botanist at the E.A.A.R.S., Amani.

#### THE ANIMAL ASSOCIATION.

Of wild animals nothing larger than porcupines, hyraxes, mongooses and rats is stated to occur in the valley. The two European farms carry about a hundred head of cattle, a few sheep and donkeys, and about fifty pigs, all of which spend the hours of daylight grazing out of doors.

At the time of our visit lepidoptera were very scarce, mosquitoes and house-flies practically non-existent. In fact no pests except ticks made themselves apparent. Small grasshoppers abounded in the grassland.

#### THE BIRDS.

The names given below and their order follow the *Systema Avium Ethiopicarum* so far as possible, Part II not yet having reached us. No collecting was done. Trinomials where inserted are based either on analogy with specimens collected at Amani (which is less than 30 miles away) or on presumption, in cases where that is overwhelmingly strong on geographical grounds. The field-notes reproduced below are confined to those tending to throw light on the ecological status of each species. We should perhaps state that our experience at Amani has given us a reliable knowledge of the local birds in the field.

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The following birds were found within our area:

1. *Ardeirallus sturmii* (Wagl.). African dwarf bittern.  
A single record in swamp.
2. *Milvus migrans parasitus* (Daud.). African black kite.  
Single birds occasionally seen soaring over.
3. *Lophaëtus occipitalis* (Daud.). Long-crested hawk-eagle.  
A single bird was resident in the valley.
4. *Astur tachiro sparsimfasciatus* (Rehw.). East African goshawk.  
A pair were nesting on a ledge in the crags only a few yards outside our boundary, and the hen was sitting hard. They made remarkably few appearances over the valley.
5. *Coturnix delegorguei* (Deleg.). Harlequin quail.  
Observed only in grassland and cereals, never in bush. Estimated twenty birds.
6. *Limnocorax flavirostra* (Swains.). Black crake.  
One pair in swamp. Beyond our boundaries they were so common that there appeared to be a bird to every 100 yards of reedy stream.
7. *Actitis hypoleucos* (Linn.). Common sandpiper.  
One to three birds each day. They are said to occur at Kongei in all months of the year.
8. *Streptopelia semitorquata semitorquata*. Red-eyed dove.  
Two pairs. Usually seen in the fringing vegetation and the trees round the farms.
9. *Streptopelia capicola*. Ring-necked dove.  
One pair. Distribution as the preceding.
10. *Tympanistria tympanistria fraseri* (Bp.). Tambourine dove.  
Two pairs.
11. *Vinago wakefieldii wakefieldii* (Sharpe). Wakefield's green pigeon.  
Three once seen. Not resident.
12. *Centropus superciliosus*. White-browed coucal.  
Two pairs in open bush; a third pair were beginning a nest—largely of the sheaths of maize-cobs—a few feet above the ground in the bamboo clump. This pair worked only in the morning and spent their day in the fringing vegetation.
13. *Lophoceros erythrorhynchus erythrorhynchus* (Temm.). Red-beaked hornbill.  
Once seen. This bird is non-resident, and a visitor occasional enough to be called by the local Wa-Shambara the "Ndegeya Habari," the News-bird, and regarded as the forerunner of a guest.
14. *Micropus apus apus* (Linn.). Common swift.  
A single bird on September 15th, and large numbers on several afternoons from September 19th onwards. They always made themselves apparent about four in the afternoon, but we have no reason to suppose they were present during the day. We have no hesitation in regarding these very large dark swifts as European birds on migration (cf. Meinertzhagen's record, *Ibis*, 1922, p. 36, of a large flock at Korogwe, only a few miles from Kongei, on September 3rd).
15. *Micropus caffer struebelii* (Hartl.). Abyssinian white-rumped swift.  
Four birds which only appeared for about half an hour at sunset and apparently spent the rest of the 24 hours in two retort-shaped mud nests presumed to have been built by *Hirundo puella*.
16. *Colinus striatus affinis* (Shelley). East Coast speckled mousebird or coly.  
Probably about forty-eight individuals. They inhabited the avenues and orchards and made occasional excursions into the open bush. They were practically always in small parties of not more than half a dozen. A few birds were beginning to collect nesting-materials.



17. *Trachyphonus vaillantii suahelicus* (Rehw.). East African Levaillant's barbet.

A single pair. These bizarre birds divided their time between the trees of the fringing vegetation and those surrounding Kongei farm-house. The male "sang" throughout the hours of daylight and about September 22nd his mate began to sit in a hole in a tree.

18. *Dendropicos lafresnayi hartlaubii* (Malh.). Greenbacked cardinal woodpecker.

Apparently only a single pair, which ranged through all the trees.

19. *Hirundo smithii smithii* (Leach). Wire-tailed swallow.

A pair round one farm-house and another pair with two young just out of the nest on the other.

- [20. *Hirundo puella unitatis* (Sol.). Striped-breasted swallow.

Two retort-nests occupied by swifts (*M. c. struebelii*, cp. No. 15) appeared to belong to this species, although they were not quite typical, in that they were stuck on the wall back to back. We never saw a *puella* at Kongei, but our experience at Amani has led us to regard this species as a well-marked seasonal migrant absent from the Usambaras from July to the end of September.]

21. *Riparia fuligula rufigula* (Fsch. and Rehw.). Brown-throated rock martin.

Four pairs, each with two young in the nest, round one farm; no occupied nests round the other. From the numbers seen on the wing at once, the total fully-fledged *Riparia* population of the valley must have been about a score.

22. *Riparia riparia riparia* (Linn.). Common sand martin.

Three, apparently European, sand martins appeared on September 29th.

23. *Hirundo monteiri* (Hartl.). Giant swallow.

There were several present every day hawking over the grassland or perching, as is their habit, on the branches of the same small tree. Average number present, 8.

24. *Alseonax minimus roehli*. Forest flycatcher.

Six birds noted, mostly in the closed bush.

25. *Platysteira peltata peltata* (Sund.). Kilimanjaro wattle-eyed flycatcher.

Two pairs; confined to the orchard and the closed bush, respectively.

26. *Laniarius ferrugineus sublacteus* (Less.). Black-winged pied shrike.

Two pairs in the closed bush and thicker open bush. They were heard very much more than they were seen, the male with his loud high-pitched double bell-note and the female uttering in antiphony a deep growling groan. The latter takes up her cue so perfectly in time that it is difficult to realise that the whole performance is not the work of a single bird.

27. *Dryoscopus cubla hamata* (Hartl.). East African puff-backed shrike.

One pair in the closed bush.

28. *Fiscus collaris humeralis* (Stanley). Abyssinian fiscal shrike.

A strongly dominant species represented by thirty-two birds, the majority of them paired. They were based on the avenues and on the isolated trees from which they hawked down onto the grassland or into the market-garden crops. They made excursions into the open bush but shunned the closed bush, presumably because they are ground-feeders. Both a vantage-point of some sort and ground clear of undergrowth are evidently necessities for this species, but in the grassland even a thorn-shoot 6 inches high met the first requirement.

To a small extent this bird impales its prey and it appears to concentrate on grasshoppers. Two nests with young in the last week in September, both in low acacias in the grassland.

29. *Corvus scapulatus* (Daud.). White-bellied raven.

Only once seen. Experience at Amani inclines us to think that this and the next species are mutually exclusive.

30. *Corvus albicollis* (Lath.). White-necked raven.

A pair, probably resident on the remoter crags, were a scourge to the poultry.

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31. *Oriolus oriolus oriolus* (Linn.). European golden oriole.

A flock of eight males passed over on September 11th.

32. *Oriolus larratus* (? subsp.). Black-headed oriole.

One pair in the shelter belt.

33. *Buphaga erythrorhyncha* (Stanley). Red-billed oxpecker.

The number of these birds that seemed to find sustenance in the valley was extraordinary. They appeared to rely wholly on what they could find on the bodies of the stock and we never saw them foraging on the ground, yet an average number of twenty-one of these large birds were in constant attendance on the hundred head of cattle, supplemented by the few sheep, pigs, and donkeys, that the valley contained. We have counted as many as thirty-eight oxpeckers on sixty head of stock. The local veterinary authorities regard these birds as an unmitigated pest. It is stated that they pay little attention to any parasites the cattle may be harbouring, but concentrate on wounds and sustain themselves mainly on the raw tissue of the animals. It appears however that a detailed investigation into the food of oxpeckers in East Africa remains to be made.

A split in an outcrop of rock in the middle of the grassland contained two young hatched September 10th. Five days later they had disappeared. On September 29th three more eggs had been laid on the same mass of hair and wool.

34. *Pholidauges verreauxi* (Finsch. and Hartl.). White-breasted purple starling.

Once seen in the orchard.

35. *Otyphantes reichenowi* (Fschr.). Reichenow's black and yellow weaver.

Seventeen pairs, one with two young on the wing. The other pairs practically all had nests, often more than one, and most of them still green. The number of fresh nests visible is no guide to the number of birds present. These, like some other weavers, appear to build nest after nest, just as some women knit unnecessary garments. One pair built three nests in the same tree in a fortnight.

All these seventeen pairs were strictly sedentary, living in the avenues and the trees in the fringing vegetation with excursions into the open bush. It is possible that these birds were "holding territory." Their rasping chirp of challenge was regularly encountered at almost the same spots. All the nests were at least 10 feet from the ground, which would seem to rule out the open bush as a breeding habitat.

This weaver has a catholic taste in food; stomachs examined at Amani have contained maize, cinnamon berries and insects. They are partial to ants.

36. *Hyphanturgus ocularius suahelicus* (Neum.). East African spectacled weaver.

Five pairs; three nests located within 8 feet of the ground in the orchard, the fringing vegetation and open bush.

In this species, also, insects are freely taken as well as grain.

37. *Xanthophilus aureocephalus* (Smith). Brown-faced olive-golden weaver.

It was surprising to find this weaver, which in the *Vögel Afrikas* (1905) is regarded as a close associate of coconut palms, the commonest species at Kongei, which is many miles from any coconuts. At least sixteen parties averaging ten birds each of all sexes and ages inhabited the valley, based on the trees, especially the avenues, from which they made excursions into the open bush. It is a remarkable fact that they paid practically no attention to the ripe barley and the ripening rye; although it was affirmed to us that in a previous year half a crop of wheat had been destroyed by "these yellow birds." It seems possible that the beard on the barley and rye may deter them. About a dozen very fresh green nests were located.

- [38. *Amblyospiza albifrons unicolor* (Fschr. and Rehw.). Black swamp weaver.

Four nests of the year in an isolated patch of *Cyperus* about 6 yards in diameter. The absence of the owners is in accordance with seasonal movements observed at Amani.]



39. *Spermestes nigriceps* (Cass.). Brown-backed manikin.  
Two small parties of about ten each in open bush.
40. *Hypochera* (? sp.). Blue-black finch.  
In open bush.
41. *Coccyphygia melanotis kilimensis* (Sharpe). Grey-headed grass finch.  
Two pairs, one building, in open bush.
42. *Estrilda astrild minor*. Red-eyebrowed grass finch.  
Parties of a dozen or more not uncommon in the open bush and also on the standing maize stalks from which the cobs had been plucked.
43. *Sorella emini* (Hartl.). Chestnut sparrow.  
One pair of what appeared to be this species in the closed bush.
44. *Poliospiza striolata affinis* (Richm.). Southern streaky serin.  
Occurred in the open bush in small parties.
45. *Spinus citrinelloides hypostictus*. Streaky green serin.  
Not uncommon in the open bush.
46. *Emberiza major* (Cab.). Yellow-breasted bunting.  
We are not clear about the status of these birds in the valley. Two pairs were noted on September 19th, but it is doubtful if we should have missed such conspicuous birds for 10 days had they been resident—as they are at Amani.
47. *Anthus* (? sp.). Pipit.  
Two birds seen only on September 18th had the air of being migrants.
48. *Pycnonotus tricolor micrus* (Oberholser). Yellow-vented bulbul.  
A very flourishing species. The probable number inhabiting the valley was eighty. They were based on the orchard and avenues, making excursions into the open bush.
49. *Zosterops flavilateralis* (Rchw.). Coast pale white eye.  
Itinerant flocks of as many as forty birds were occasionally met with.
50. *Zosterops massaica* (van Som.). Teita white eye.  
One bird corresponding to the description of this species in closed bush.
51. *Cinnyris bifasciatus microrhynchus* (Shelley). Little red-banded black sunbird.  
One pair in open bush.
52. *Cinnyris gutturalis inaestimata* (Hart.). Red-breasted sunbird.  
Four pairs, two of which were incubating. They divided their time between the orchard and the fringing vegetation.
53. *Cinnyris mediocris usambaricus* (Grote). Olive-bellied sunbird.  
Three pairs in open bush; one nest with eggs.
54. *Anthreptes collaris elachior* (Mearns). Little yellow-bellied sunbird.  
One pair in the closed bush.
55. *Parus fringillinus* (Rchw.). Large buff-breasted tit.  
Once seen in the trees of the shelter-belt.
56. *Cisticola erythrops sylvia*. Rufous-bellied fan-tailed warbler.  
Not uncommon in the open bush.
57. *Apalis* (? cinerea) (Sharpe). Grey forest warbler.  
One bird apparently of this species in the closed bush.
58. *Prinia mistacea immutabilis (tenella)* (Cab.). Coastal wren warbler.  
Not uncommon in the open bush.

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59. *Crateropus jardinei hypostictus* (Cab. and Rehw.). Babbler.

Six birds observed in open bush. A pair were incubating in a nest just outside our boundary.

60. *Cossypha heuglini intermedia* (Cab.). Coastal white-striped cossypha.

At least six birds in the valley. Confined to the orchard and the open bush. The startling passionate song was uttered for only a few minutes at dawn and after sunset; and from the increase in volume towards the end of September the birds were presumably preparing to breed.

61. *Bradypterus* (? sp.). Swamp warbler.

One in swamp.

62. *Saricola torquatus axillaris* (Shelley). East African stone chat.

One pair in open bush.

In addition, the following species were observed just outside our boundary:

*Turacus hartlaubi* (Fsch. and Rehw.). Blue-crested plantain eater.

*Thamnolaea subrufipennis* (Rehw.). Rufous-bellied mountain chat.

*Vidua serena* (Linn.). Common pied whydah.

A single specimen only in each case.

*Motacilla aguimp* (Dumont). African pied wagtail.

A family party.

### SUMMARY AND DISCUSSION.

1. Sixty-two species in all were recorded within the valley, of which twelve cannot be regarded as in any sense residents. Of the resident species those for which we are able to give statistics are represented by about 550 (548) individuals in all. We think that, for the species it concerns, this is a reliable figure. Making a generous allowance for the number of migrants and of itinerant birds (such as *Zosterops flavilateralis*) supported by our area at any given time, and of those bush-dwelling species for which we have not been able to get statistics, we arrive at a density of population of the order of three birds to the acre at the outside, taking the area as a whole.

2. It may be interesting to compare this result with the following figures quoted by Nicholson (*How Birds Live*, 1927, App. 3), for breeding, or at any rate settled, bird populations.

Locality	Area in acres	No. of birds	No. per acre
U.S.A.			
Pennsylvania...	640	About 1176	About 1.83
Illinois ...	640	" 600*	" 0.90
North-east: Woodlands†	100	" 350	" 3.50
North-east: Farms†	100	" 238	" 2.38
Washington, D.C. (Suburban estate)	5	" 270	" 54.00
ENGLAND			
Kent ...	5120	" 3300	" 0.67
Kent ...	2560	" 1560	" 0.60
New Forest, Hants.†	11	—	" 21.00
Haslemere, Surrey	40	" 290	" 7.25
		adults (reared 453 young)	

\* Aboriginal species only.

† To be accepted with caution.

‡ This was an island site, copse and arable entirely surrounded by open heath, and the birds found much, if not most, of their food outside the 11 acre area.

It is unfortunate that no reliable published figures are available for exactly comparable "mixed farm" land in the Temperate Zone. Mr Nicholson tells us that he considers a density of "one to two birds per acre" approximately normal for farm lands in Western Europe.

3. The Kongei figure of three birds to the acre conceals a great difference in density within the area itself. More than half the 300 acres was ornithologically almost a desert. The 150 acres of grassland, which as will be seen from the description is singularly homogeneous, devoid of weeds and cropped short, supported (a) directly, part of the twenty quail, (b) indirectly, twenty-one oxpeckers, (c) partially, thirty-two fiscal shrikes; equivalent in total to not more than one bird to three acres. The 30 acres of cereals, however attractive it might be at other seasons, or under other crops, can only be credited with supporting, at the time of our study, a few quail, and attracting a slight amount of attention from *Xanthophilus aureoflavus* and *Estrilda*. On the 25 acres of freshly ploughed land we never saw a bird feeding except a single *Centropus*. Again, the 24 acres under market-garden crops were remarkably devoid of bird-life. In England half-a-dozen species would have resorted to them at any season of the year. At Kongei they seemed to attract nothing but the fiscal shrikes, and, to a very limited extent, the bulbuls. It is possible that this may be due in part to the aggressiveness of the shrikes, which in our own garden at Amani tend to drive away other birds. On the other hand, the orchards, shelter belts and avenues teemed with birds, while the fringing vegetation assumed for the birds an importance out of all proportion to its insignificant area. The bush occupied an intermediate position, being much more populated than the grassland, cornland, market-garden and plough, but less so than the areas carrying trees.

Generally speaking, the impression gained was that the bird population of the valley would have been a great deal poorer in numbers if introduced trees had been absent. We were unable to do any quantitative work on the typical native-farmed areas surrounding Kongei, but there is no doubt that the five most numerous species in our valley, which together made up nearly half its entire population (*Xanthophilus aureoflavus*, 160 birds; bulbuls, 80; colies, 50; *Othyphantes reichenowi*, 34; fiscal shrikes, 32) were not nearly so much in evidence elsewhere in the district.

Considering the list of species qualitatively, we have been struck by the remarkable omissions. There are no drongos (*Dicrurus*), nor dry-feeding kingfishers (e.g. *Halcyon albiventris*), both of which are characteristic of the clearings at Amani; no bee-eaters, no starlings (excepting the specialised oxpeckers), both of which are usually well represented in dry areas; no wagtails, which might have been expected to be well provided for by the water-courses, the cattle and the vegetable patches.

We are tempted to suggest that the adaptation of the bird population to the changed conditions in the valley (and in the surrounding cleared areas) has

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been imperfect, with the result that the area is "carrying" fewer birds than it might. The avifauna characteristic of the rain forests has been swept away with them without leaving a trace. Practically no rain forest species has lingered, has adapted itself to the new conditions, or has been attracted by the growth of the introduced trees to re-colonise the valley. (Though a few miles away *Arizelocichla milanjensis striifacies* maintains a footing in the threadbare vestiges of forest, hardly worthy of the name, along the Mombosoni gorge.) On the other hand, there has been no striking incursion of a dry-country avifauna—such as *Trachyphonus d'arnaudii böhmi*, *Macronyx ameliae wintoni*, *Spreo superbus*, all of which are characteristic of the thorn country a few miles away to the south—although there are species in the Kongei list that indicate a tendency in that direction. *Trachyphonus vaillantii suahelicus* belongs to the thorn-bush south of the Pangani, its presence at Kongei constituting an extension of its recorded range; and if the occurrence of *Sorella emini* is confirmed this is also an invader from steppe countries. The 50 years since the clearing of the forest round Kongei might seem a long enough period for the bird population to adjust itself fully to the changed conditions; but there is also near Amani another grass area, of very different type, which, although older than that at Kongei, has failed to attract what one would consider an appropriate bird population.

It would be interesting to re-examine the Kongei valley at intervals of 5 years, and ascertain whether or no the bird population is in a transitional state.

# THE INFLUENCE OF SECTIONAL GRAZING AND MANURING ON THE FLORA OF GRASSLAND

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(*With seven Graphs and four Diagrams.*)

## INTRODUCTION.

THE present investigation arose while the writer was doing advisory work on grasslands in the south-west of England. During the year 1927 several experiments were laid down to test the sectional method of grazing grassland (6). Two of these experiments were studied during the year 1927, the botanical changes in the flora noted, analyses being made periodically. Unfortunately, the writer left the district in November of 1927, and further observations were not possible. Fortunately Mr F. R. Horne, M.A., has kindly supplied details for one of the plots at East Devon for the month of December 1929. The information supplied shows that there has been no material change in the important species of the vegetation. Unfortunately, the treatment at Knight's-Hayes has been discontinued, and further information from that source is no longer possible.

The two experiments dealt with in this investigation were at East Down on the farm of Seale-Hayne Agricultural College, Newton Abbot, Devon; and at Knight's-Hayes, near Tiverton, Devon; the latter on the property of Sir Ian Amery. Mr C. D. Ross, B.Sc. (County Organiser) conducted the Knight's-Hayes' experiment. The East Devon experiment was conducted by the Agricultural Department of Seale-Hayne Agricultural College. Both experiments were run in conjunction with Messrs Nitram, Ltd. The rainfall in both areas varied from 35 to 40 in. per annum. Both fields had complete manurial dressings applied before the sulphate of ammonia applications commenced. As soon as the stock were moved from a plot the droppings were spread and the sulphate of ammonia applied. The grazing was so handled that as soon as the last plot was grazed the first was ready for re-grazing.

The investigation is concerned with the botanical changes following the application of the sectional method of treatment. The agricultural aspect is dealt with only in so far as it affects directly and indirectly the flora of the grassland.

### *Knight's-Hayes.*

The field at Knight's-Hayes is, except at the west corner, level. Previous to this experiment the field had been a water meadow and irrigated. The general treatment had been to cut for hay and graze later in the year. This

is quite a common practice in many parts of Devonshire. The usual result of this practice is to depress Wild White Clover and in the later part of the year to encourage Bent Grass (*Agrostis palustris* Huds.). Another possibility is that, unless the irrigation is carefully controlled, Yorkshire Fog (*Holcus lanatus*) will show a large increase, while if the amount of water is too small, Crested Dogtail (*Cynosurus cristatus*) and Sweet Vernal (*Anthoxanthum odoratum*) may spread to a considerable extent. Mismanagement of the grazing will increase weeds and less valuable grasses, and decrease clovers and useful grasses. Unless the drainage is good moss will spread rapidly during the winter and colder parts of the year, and Buttercups will also tend to spread. Should the field be too heavily stocked during the wet spells the soil will get "puddled," and Daisies spread rapidly.

As far as the contour of the field is concerned Plots 1 and 2 are on very level ground. The east side of Plot 1 is, however, slightly higher than the old irrigation channel running just inside the west side of the plot; while Plot 2 is slightly below this level and would tend to get a little more moisture. This is borne out by the higher proportion of Meadow Foxtail in Plot 2. Plot 3 is at a higher level than Plots 1 and 2, except a strip at the side of Plot 2. This plot is also rather irregular owing to two large water channels running across its length and another connecting them. Owing to these channels being fairly deep, although never artificially filled, after heavy rain they remained full for some time. This tended to make the edges of these channels wet and affect the vegetation, while the tramping of cattle broke them down and released the water. The general effect of this, as will be seen, was to hinder the progress and improvement of this plot and render it of less value than 4 and still less than 1 and 2. With the continuous and regular treatment, however, this plot improved very much and, at the conclusion of the experiment, was not very far behind the others.

Plot 4 was the most irregular of all. The extreme corner was much the highest part of the whole field, while the far north-west corner next the G.W.R. line was the lowest. An irregular channel ran obliquely across it to join those in Plot 3. This was fringed with Stinging Nettles and later with *Polygonum* spp. The lowest part of the field had many scattered rushes but no clumps. In spite of this irregularity and the fact that generally the plot rose steadily above the level of 3, the vegetation was good and, at the beginning of the experiment, contained fewer weeds than the other plots. At the end it was quite as good as Plot 2. The explanation of this is that the slope was such as to run off excess of water, even any overflowing from the irrigation channel quickly drained to a still lower level. In fact, in this respect it had a slight advantage over any of the other plots. During the dry spell in the spring it never scorched in the higher parts. This was doubtless due to moisture slowly percolating down from a channel at the higher end of the plot, while the orchard on still higher ground above must have conserved much moisture



for the dry periods. This obviated the "drought patches" so characteristic of many Devonshire grasslands situated on sloping ground.

*East Down.*

This field sloped south-east by east with an elevation of about 450 ft. Five plots were fenced off parallel to each other. Previously the field had been in grass for many years. For a considerable time it was undergrazed, but more recently was laid up for hay and then grazed. The vegetation, although superior to many of the permanent pastures in the district, had a large number of species present, while there was a higher proportion of Bent Grass, Yorkshire Fog, and an appreciable amount of Golden Oat Grass. The soil was a loam and, in spite of a good rainfall, the drought in summer invariably affected the vegetation. The reason for this was that in places the underlying shillit (shale) came near the surface soil.

METHOD OF ANALYSIS.

The method of analysis was the grid method as used by Armstrong (1) and Stapledon (10). The grid used was 10 in. square and subdivided into square inches by cross wires. Frequent readings were taken across the plots and the readings totalled. The figures given are the averages. In all cases the individual readings showed little difference from the average. The grid method was adopted so as to make a suitable comparison with other work (1), (10), particularly in Devon (2).

From time to time areas of the plots (at Knight's-Hayes) were fenced before the cattle and sheep were turned into the plot. Cuttings of these were taken and the herbage was sorted out and the proportion by weight of the dry material was estimated (Table II). The herbage thus analysed was dried slowly in the laboratory. Unfortunately, it was not possible to visit the plots very frequently and, therefore, the ungrazed material fenced off was much longer than the vegetation the stock grazed. This explains the rather high proportions of certain of the grasses when comparing the ungrazed material with the grazed. It must be pointed out, however, that for reasons of economy the fences for the "long grass" were placed next the plot boundary fences. In the case of Plot 2 this was rather unfortunate, since this part received extra moisture from the channel in Plot 3. This is reflected in the high and rather flattering figure achieved by Meadow Foxtail in the analyses for May 13th and June 1st. The analyses by weight were done by my assistant, Mr C. A. Cosway, B.Sc.

The dates on which the plots were examined were determined largely by the rate of growth of the plots and the rate of change of the vegetation. As the season advanced the herbage settled down on all the plots to a fairly fixed proportion. Visits latterly were not so frequent, and on several occasions the readings were practically identical with those previously recorded. When this occurred, no further readings were taken till after another spell of grazing and manuring, when changes in the vegetation were evident.



## CONDITIONS OF THE PLOTS DURING THE SEASON.

*April. (Table I.)*

The first visit enabled one to form a good idea of the field which was being portioned off into four plots. The general impression was that the stock tended to be more on the area to become Plot 1, as it was near the entrance gate. This was also indicated by 12 per cent. being bare, 12 per cent. moss-covered, Daisies were 6 per cent. (the highest per cent. present in any of the plots), while Wild White Clover was 15 per cent. The area for Plot 2 showed much the same vegetation as Plot 1, but like 3, Bent was rather high. Meadow Foxtail was highest in this plot. Plot 3 did not vary very much from Plot 2, perhaps the most interesting features being the presence of 3 per cent. *Plantago lanceolata* and 2 per cent. *Luzula campestris*. These occurred on the higher parts of the plot. Plot 4 was rather interesting, since not only did it contain fewer ingredients of a reasonable proportion, but Yorkshire Fog (13 per cent.), Crested Dogtail (10 per cent.) and Sweet Vernal (10 per cent.) were considerably higher than in the other plots. At first one might consider that the high proportion was due to more moisture. Had this been the cause then part of Plot 3 should have given about the same proportion, but this was not the case. The real explanation lies in the contour of the area and the fact that it would not be possible to cut much of it with a mower. If cut it would have to be with a scythe. In short, as usually happens in such cases, the cutting is more to keep down top and rank growth than for hay. As we have found in many other instances this is just the condition, where no intensive grazing follows, which gives these grasses the chance to get the upper hand (5). A certain amount of grazing has occurred, as is shown by the proportion of Rye Grass and of Wild White Clover, but not sufficient to keep coarser growth in check.

It was quite evident that, during the autumn of 1926 and the following winter, Bent had formed a considerable proportion of the herbage, since many traces of its presence could be found, both dead leaves and inflorescences. The tall growth in spring and early summer, however, when the herbage is allowed to grow for hay, generally tends to hold this grass in check, and prevent Bent becoming the dominant grass, which it frequently is on grasslands grazed and never cut. In meadows in poor condition Bent may form a high proportion of the hay (3).

*April 22nd. (Tables I and II.)*

It will be seen from Table II that the plots were showing their first flush of growth after treatment. Rye Grass was dominant, but Yorkshire Fog and Bent gave very high yields of the proportion. This is brought out in the analysis by weight of the ungrazed herbage samples taken from Plot 3. Wild White Clover was just beginning to show growth, but was rather held in check by the grasses. The grazing had not been in action long enough to keep the grasses

Table I. *Knight's-Hayes, 1927.*

Plots	Ground covered %											
	April 2nd				April 22nd				May 13th			
	1	2	3	4	1	2	3	4	1	2	3	4
Wild White Clover ( <i>Trifolium repens</i> )	...	15	6	8	6	14	15	3	11	23	8	6
Red Clover ( <i>T. pratense</i> )	...	...	...	...	...	...	...	...	...	...	...	...
Yellow Suckling ( <i>T. minus</i> )	...	...	...	...	...	...	...	...	...	...	...	...
Perennial Rye ( <i>Lolium perenne</i> )	...	31	30	30	30	33	28	25	45	38	32	36
Cocksfoot ( <i>Dactylis glomerata</i> )	...	3	3	...	4	4	1	12	...	2	1	1
Timothy ( <i>Phleum pratense</i> )	...	t.	1	...	...	1	1	5	4	1	3	4
R.S. Meadow Grass ( <i>Poa trivialis</i> )	...	4	1	2	...	1	1	...	...	...	...	...
Meadow Fescue ( <i>Festuca pratensis</i> )	...	...	...	...	...	1	1	2	3	5	3	5
Meadow Foxtail ( <i>Alopecurus pratensis</i> )	...	t.	4	2	t.	3	t.	t.	6	8	4	5
Crested Dogtail ( <i>Cynosurus cristatus</i> )	...	2	8	5	10	...	...	...	9	9	11	9
Sweet Vernal ( <i>Anthriscanthum odoratum</i> )	...	3	8	4	10	12	16	10	2	t.	4	6
Bent ( <i>Agrostis palustris</i> , Huds.)	...	5	12	10	8	21	22	35	13	4	20	15
Yorkshire Fog ( <i>Holcus lanatus</i> )	...	3	1	3	13	...	...	...	...	...	3	...
Yarrow ( <i>Achillea millefolium</i> )	...	...	...	...	...	1	t.	...	...	...	...	...
Plantain ( <i>Plantago lanceolata</i> )	...	...	3	5	...	3	5	...	...	...	...	...
Hawkweed ( <i>Hieracium</i> spp.)	...	6	1	3	...	1	3	...	t.	...	...	...
Daisy ( <i>Bellis perennis</i> )	...	...	...	...	...	1	5	5	5	6	5	6
Buttercup ( <i>Ranunculus repens</i> )	...	3	6	3	5	...	...	...	...	...	...	...
Thistle ( <i>Cirsium arvense</i> )	...	...	...	...	...	...	...	...	t.	t.	t.	t.
Dock ( <i>Rumex</i> spp.)	...	...	...	...	...	...	...	...	2	...	...	...
Chickweed ( <i>Cerastium triviale</i> )	...	...	...	...	...	...	...	...	...	...	...	...
Rushes ( <i>Juncus communis</i> )	...	...	...	...	...	...	...	...	...	...	...	...
Wood Rush ( <i>Luzula</i> )	...	...	...	...	...	...	...	...	...	...	...	...
Geranium ( <i>Geranium</i> spp.)	...	1	...	...	...	t.	1	2	t.	t.	t.	3
Sorrel ( <i>Rumex acetosa</i> )	...	...	...	...	...	1	1	t.	...	...	...	...
Sedge ( <i>Carex</i> spp.)	...	12	8	12	10	3	1	...	...	...	...	...
Moss ( <i>Musc</i> spp.)	...	12	8	8	4	...	...	...	...	...	...	...
Bare	...	...	...	...	...	...	...	...	...	...	...	...
Dandelion ( <i>Taraxacum officinale</i> )	...	...	...	...	...	...	...	...	...	...	...	...
Self Heal ( <i>Prunella vulgaris</i> )	...	...	...	...	...	...	...	...	...	...	...	...
Cuckoo Flower ( <i>Cardamine pratensis</i> )	...	...	...	...	...	...	...	...	...	...	...	...
Soft Brome ( <i>Bromus mollis</i> )	...	...	...	...	...	...	...	...	...	...	...	...

t. = trace.

in check and give the clover a chance. A most noticeable feature is the marked fall of Sweet Vernal and Crested Dogtail. The reason for the apparent discrepancy between the analysis weight and by percentage ground covered in the case of Bent and Yorkshire Fog is due to the fact that Bent was grazed and Yorkshire Fog hardly touched.

Table II. *Knight's-Hayes, 1927.*

Plots	Hay, % by weight.					
	April 22nd	May 13th		June 1st		August 23rd
	3	1	2	1	2	3
Wild White Clover ( <i>Trifolium repens</i> ) ...	0.34	2.54	10.55	11.36	9.69	6.16
Red Clover ( <i>T. pratense</i> ) ...	—	—	—	—	—	0.27
Perennial Rye ( <i>Lolium perenne</i> ) ...	34.16	32.12	38.42	52.59	38.10	43.62
Cocksfoot ( <i>Dactylis glomerata</i> ) ...	8.54	—	—	—	—	—
R.S. Meadow Grass ( <i>Poa trivialis</i> ) ...	7.51	12.51	2.59	3.31	0.83	1.85
Meadow Fescue ( <i>Festuca pratensis</i> ) ...	—	—	—	6.29	7.87	2.47
Meadow Foxtail ( <i>Alopecurus pratensis</i> ) ...	1.93	0.75	16.66	10.14	15.57	6.16
Crested Dogtail ( <i>Cynosurus cristatus</i> ) ...	—	7.44	7.41	4.52	7.87	—
Sweet Vernal ( <i>Anthoxanthum odoratum</i> ) ...	2.48	7.27	7.96	2.98	12.86	9.11
Bent ( <i>Agrostis palustris</i> , Huds.) ...	19.14	9.30	1.95	3.20	0.15	14.24
Yorkshire Fog ( <i>Holcus lanatus</i> ) ...	18.25	19.86	10.74	2.43	5.38	16.10
Daisy ( <i>Bellis perennis</i> ) ...	—	0.25	0.37	2.21	—	—
Buttercup ( <i>Ranunculus repens</i> ) ...	1.24	2.20	3.06	—	0.66	—
Geranium ( <i>Geranium</i> spp.) ...	—	—	—	2.54	—	—
Sorrel ( <i>Rumex Acetosa</i> ) ...	6.40	0.17	0.18	2.21	0.91	—
Cuckoo Flower ( <i>Cardamine pratense</i> ) ...	—	—	—	—	0.15	—
Soft Brome ( <i>Bromus mollis</i> ) ...	—	—	—	2.21	—	—

*May 13th. (Table I.)*

By this date the effects of manurial dressings and the regular rotation of grazing animals were reflected in the gradual settling down of the vegetation to a fairly homogeneous flora. Rye grass was more dominant. Bent had practically disappeared, and there was a slight increase in Sweet Vernal and Crested Dogtail due to shortness of the vegetation. Yorkshire Fog showed a marked decrease, and it was being grazed better. Weeds were not so frequent, with the exception of Buttercups, but they frequently show an increase during the early stages of grassland improvement. Wild White Clover shows a marked increase on all plots, this being a sure indication along with the high proportion of Rye Grass that the herbage is improving. Another feature was the appearance of Wild Red Clover. The order of the plots at this date was first Plot 2, second Plot 1, third Plot 4, and last Plot 3.

The vegetation which had been kept from the stock and analysed by weight is shown in Table II. It will be noted that Yorkshire Fog is high; this is due to the disinclination of the stock to graze it during the early stages. The high proportion of Meadow Foxtail in Plot 2 has been previously explained.

*May 20th.*

An examination of the plots revealed no material change in the composition of the herbage. The rather dry period during the spring doubtless accounted for this state of affairs.

*June 1st. (Tables I and II.)*

The stock were grazing Plot 2, and between the stock and the amount of droppings it was quite impossible to attempt anything like an accurate analysis. In general it was very similar to Plot 1.

The outstanding feature of all the plots was the high proportion of Wild White Clover and Rye Grass; in Plot 1, 73 per cent.; Plot 3, 72 per cent.; Plot 4, 58 per cent. The break in the drought had greatly refreshed the herbage, and the considerable amount of Meadow Foxtail present pointed to a good supply of fresh water. Wild White Clover had greatly increased in all the plots, and Rye Grass also showed an increase. An interesting discovery was the appearance of Meadow Fescue. A few plants had been noticed but, following on the breaking of the dry spell, Meadow Fescue seemed to get a better chance to develop and increased considerably. Yorkshire Fog had diminished and, except in Plot 4, Sweet Vernal was not very plentiful. Bent, as before, was not much in evidence.

The "hay plots" of 1 and 2 did not reveal anything very striking except that, as might be expected, those things which can grow to length tend to be flattered in a calculation by weight. The high position of Meadow Foxtail as occurred on May 13th is about the same proportion. Sweet Vernal has increased, especially in Plot 2, but this is largely due to the after-effect of the dry spell in the spring. It will be noticed that there is a marked decrease in Bent and a still greater decrease in Yorkshire Fog.

*June 27th. (Table I.)*

At this stage it will be seen from the figures in Table I that the plots show a certain amount of periodicity in the proportion of ground covered by the different species. This is quite a marked feature of many well-grazed Devonshire pastures of good quality. In such cases there is a varying fluctuation of Wild White Clover and Rye Grass, which forms usually about 70 per cent. of the herbage. After Wild White reaches a high figure, Rye Grass follows by a marked increase and the Wild White Clover decreases. This is in turn followed by an increase in Clover and a reduction in Rye Grass, and this may be repeated several times, depending on length of the growing period, the season, and the grazing.

Plot 1 is about the same, except that Rye Grass had decreased while Yorkshire Fog and Bent have increased. Plot 2 from May 13th figures has an increase in Wild White Clover and a decrease in Rye. Plot 3 shows a marked increase in Wild White Clover and a decrease in Rye, accompanied by an increase in Yorkshire Fog, Bent, and Rough Stalked Meadow Grass. Plot 4 was rather lagging behind the others in the periodicity movement, in that Wild White Clover had greatly increased but Rye had scarcely begun to show a decrease. Generally, the whole area showed a great improvement since the

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start of the experiment, but at this stage Yorkshire Fog and Bent showed signs of a tendency to increase.

*July 13th.*

An examination of the herbage revealed no marked change and, after a few test readings, no detailed examination was made. Plot 4, as previously indicated, had gone just a little further, in that Rye Grass had fallen, with a slight rise in Wild White Clover, Rough Stalked Meadow Grass accounted for the difference. The plots were far more homogeneous than they were originally, and except for the edge of the irrigation channels, show no marked diversity of herbage. Along the edges of these channels were a few Stinging Nettles, Sorrel, one tuft of Tufted Hair Grass, patches of Yorkshire Fog and Bent. But these were being regularly cut where not grazed, so that their extent was rapidly decreasing.

*August 23rd. (Tables I and II.)*

After the lapse of about 6 weeks the plots presented a very interesting appearance. Unfortunately the pipes supplying drinking water for the stock had got choked, so that the gates in all the plots were open to permit the animals to pass to any plot. This had been the case for a month previous to the examination. It was evident, however, that this had not made any material difference, as the grazing of the various plots had been equally intense. Beyond a slight lagging in Plot 4 the others had reached almost a homogeneous herbage. The reason of the lag in Plot 4 was doubtless accentuated by the wet summer; that plot getting more moisture than the others, since any sudden flush of water into the top channel would flush Plot 4 before the others were seriously affected. The figures were:

Plot	1	2	3	4
Wild White Clover ...	35	40	40	65
Rye ... ..	50	50	50	30

The rest was composed chiefly of Yorkshire Fog and Bent, with traces of the others previously mentioned, including Wild Red Clover.

*September 27th. (Table I.)*

During September there was a very heavy rainfall. Vegetation generally put on much growth during this period. In pastures it was most marked by the growth of grasses and as a result of this increase a corresponding decrease in clover. This was also evident at Knight's-Hayes, while the treading of the stock on the soft earth tended to cut up the turf in many places, especially near gateways. The plots were still grazed in general and not in the sectional method, but they were all receiving due attention. The excessive moisture, the grazing and the trampling of the milch cows on the plots brought certain of the weeds into prominence again. The last readings taken on September 27th show the state of affairs.

The figures show that by the end of September all the plots had practically the same vegetation. Plot 4 was in line with the others, in that the high proportion of Wild White Clover to Rye Grass had been reversed. There are one or two interesting points. It will be noted that Daisies occupy most space in Plot 1 and least in Plot 4. This is due to the fact that Plot 1 gets most and Plot 4 least treading. Hawkweed is least in Plot 4 and the same for the others; this is due partly to the treading and the moisture. Meadow Grass is smallest in Plot 1 as it is the driest plot, and highest in Plot 4, which is most moist owing to the irrigation channels. Buttercups follow the order of moisture content of the soil in the plots, while Yorkshire Fog does this to a certain extent. Cocksfoot does the same, but a part of Plot 1 studied accounted for 3 per cent. in Plot 1 as against 2.5 in Plot 2. Bare areas are highest in Plot 3, Plot 4 has a slight bareness, and there is not much in Plots 1 and 2 as they are there filled by moss. The bare areas are due to the cutting up of the turf by the stock, since 3 and 4 are the plots with the most moisture.

*East Down, 1927. (Graphs V, VI and VII, also Diagram I.)*

Complete details of the sectional grazing experiment at East Down are found in *Seale Hayne Agricultural College Pamphlet 26 (8)*. There are five plots, each 2 acres in extent. Botanically this experiment was interesting, as the high elevation (450 ft.) with a steady downward south-east slope caused the grassland to suffer from summer drought. This drought made recovery very slow after grazing, and particularly after the application of sulphate of ammonia. In the dry spells Wild White Clover, weeds and, to a slight extent, grasses, were scorched. So much was this the case that, on several occasions, no botanical analysis could be satisfactorily made. Another point was that, owing to the fact that some plots had an extra grazing within the drought period in their rotational succession, they suffered more than the others, while Plots 3, 4 and 5 for a time got rather too rank (8). The figures obtained illustrate the changes, and what is still more important, two grazed areas, A and B outside the plots. It is the difference between areas A, B and the plots which is of most importance in this case.

The field used for the experiment had been in grass for many years. The soil was a light loam overlying "shillit" or shale. Situated some distance from the farm it has been used for grazing, and later cut for hay. The herbage was fairly good but contained rather a high proportion of Bent Grass with appreciable amounts of Yorkshire Fog, Soft Brome and weeds. There were also one or two patches of Stinging Nettles (*Urtica dioica*), but these were strictly confined to definite patches. It may be mentioned here that at the foot of p. 6 of Pamphlet 26 (8) the word "fescues" should read "meadow grasses." Only an occasional plant of Sheeps and Meadow Fescue was present, but Rough Stalked Meadow Grass was at times plentiful.

Five plots were separated off, running from top to bottom of the field,



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leaving a considerable area on the south-west side (A) and a triangular area (B) on the north-east side, where water was available for stock in the extreme corner. Another field on the north side also opened into this triangular area (B) in order to allow the stock to have access to water. The area A was grazed pretty much on the old method, but B received much more intensive grazing and, in the shortness of the herbage due to grazing, compared with the controlled sectional plots. This enables one to obtain a reasonable comparison between (1) the old type of grazing, (2) grazing to the full capacity of the herbage, (3) sectional grazing with manuring. Plot 1, on part of the field next to Area B, is taken as typical or standard. The part of Area B, next the spring where water was available for stock, was not included in the botanical analysis, since there was not only the extra moisture possibility, but also the possibility of extra droppings of the stock. On the part examined there was no undue manuring due to this cause, although grazing was more intensive, since it lay near the water supply. The fact that the herbage in the area examined was closely grazed enabled a good comparison to be made between this area and the old method as well as the experiment, since the vegetation of this area (B) did not differ from the rest of the field at the commencement of the experiment. Another point of importance being that the area, except the north-east end of the declivity, contained no more moisture in the soil than the plots and Area A.

Graphs V and VII show that East Devon in its changes of flora closely followed Knight's-Hayes. As Knight's-Hayes has already been studied in detail further treatment of East Devon will be dealt with under Discussion.

### *East Down, 1929.*

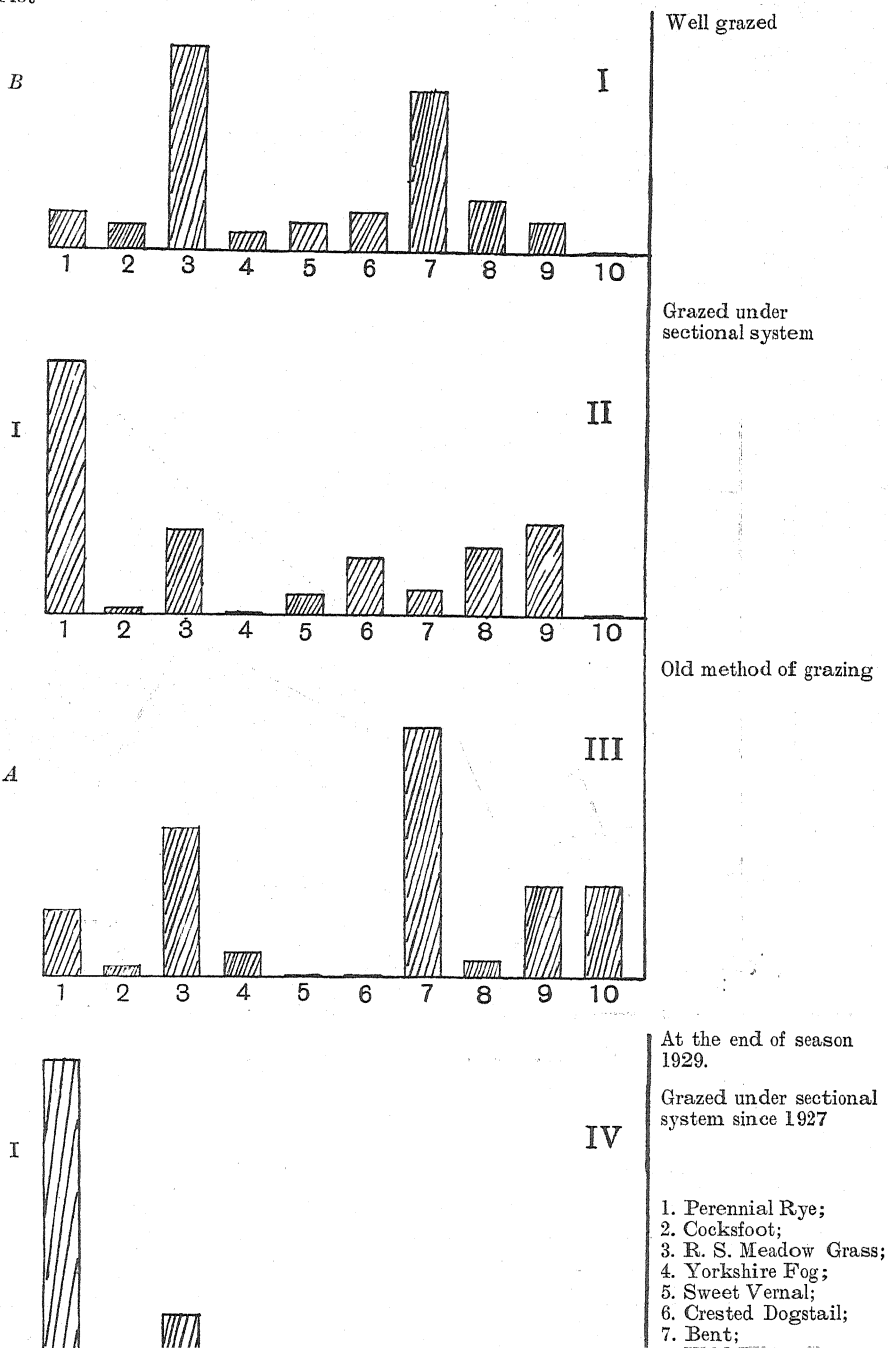
I am greatly indebted to my friend and successor, Mr F. R. Horne, M.A., for kindly supplying information and figures of the vegetation of Plot 1 in December 1929—two years after my observations were made. The species present are proportionately represented in Diagram IV. There is strong similarity to the vegetation in 1927 in spite of some fluctuations in the less dominant species of the flora. It is evident that there is little change and that the vegetation is now settled and will remain so while present treatment continues. Plots A and B are not considered, as B was too badly poached and A was rather tufted.

### DISCUSSION.

In order, first of all, to ascertain the importance of grazing as it affects the vegetation, the East Down experiment will be considered first. It will be observed that by the end of the year 1927, as the diagrams show, B ranked mid-way between Plot 1 and A. The figures show that the chief difference is in the amount of Bent, Rough Stalked Meadow Grass, Rye Grass and Wild

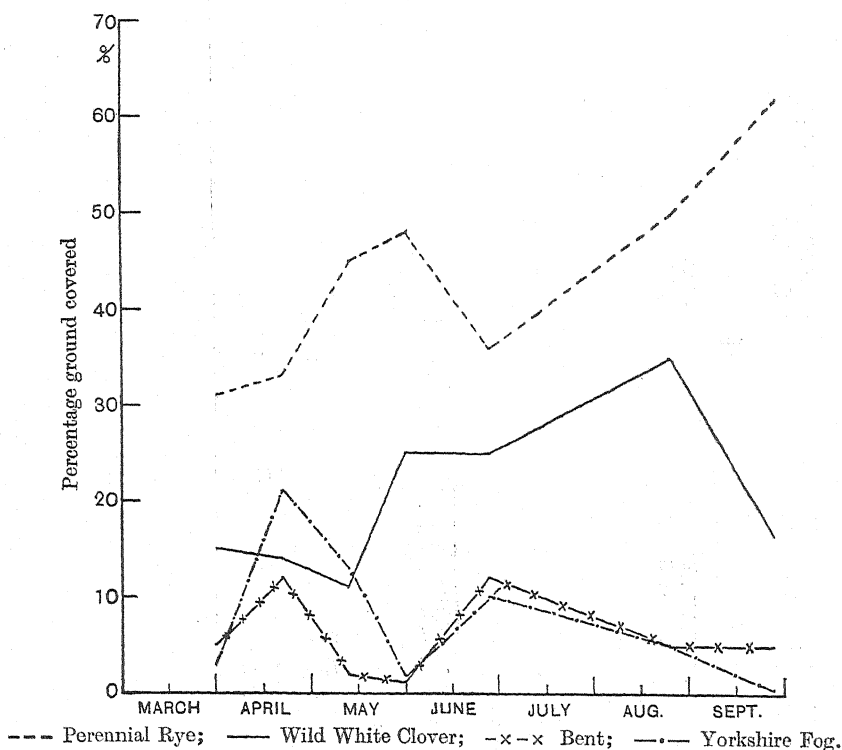
Comparison between three Areas at the end of season 1927, and one of these areas at the end of season 1929. Expressed as % of ground covered by the plants present.

Plot



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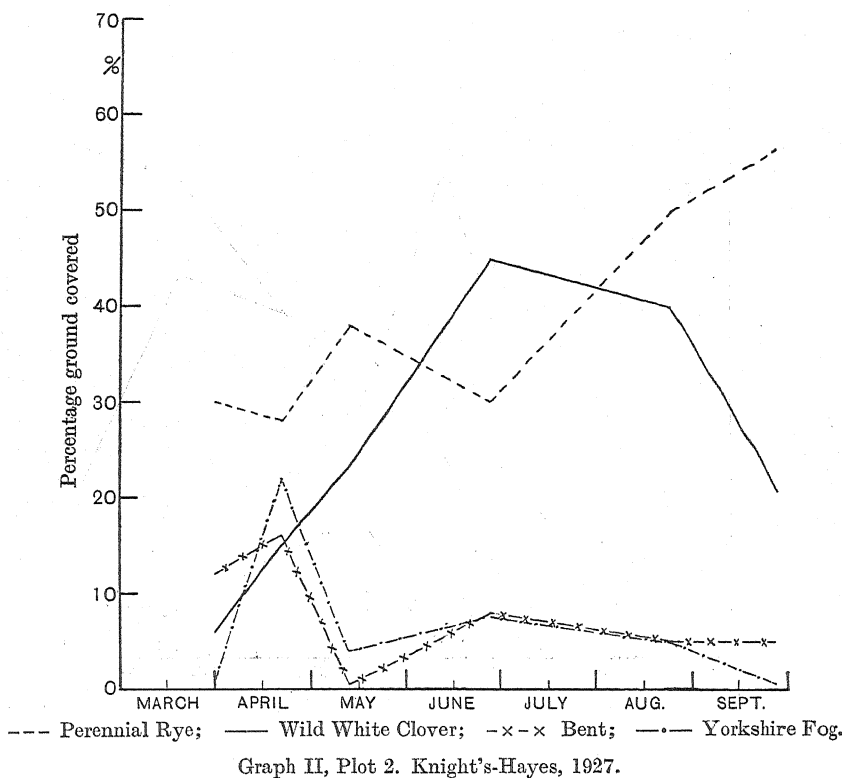
system of inadequate grazing, but decreases very much with tighter grazing, and under the sectional grazing and manuring system almost disappears. Wild White Clover shows a steady increase from A to Plot 1. Rough Stalked Meadow Grass which is affected by competition with Bent and Rye Grass is highest in B and lowest in Plot 1. In Plot 1 Rye Grass had depressed both Bent and Meadow Grass. In A Bent had depressed both Rye and Meadow Grass, but in B only Bent offered limited competition, while the considerable amount of Wild White Clover aided Meadow Grass (11). Another interesting point



Graph I, Plot 1. Knight's-Hayes, 1927.

is that, in A, Sweet Vernal and Crested Dogstail are nearly absent, due largely to the smothering action of Bent and partly also to competition with Meadow Grass. It will be noted that Yorkshire Fog has almost disappeared from Plot 1. The only other feature of interest from the figures is that weeds seem remarkably high in Plot 1. This is due to the fact that weeds include Dandelions, Yarrow, and Ribwort Plantain, which got a good opportunity with the close grazing, and owing to the greater moisture-holding capacity with no bare space, Buttercups (*Ranunculus repens*) accounted for

These figures indicate that much of the fundamental importance in the sectional grazing and manuring method is due to grazing (4). Although B is distinctly behind Plot 1, yet it obviously occupies an intermediate position; that is clearly shown by the steady increase in Wild White Clover and the marked decrease in Bent. The Rye and Meadow Grass proportions are largely affected by Bent and Wild White Clover. The chief difference between B and Plot 1 is, that with manuring, the intensity and amount of growth was increased. If the intensive grazing is added to this it is obvious that the improvement shown between A and B is speeded up, with the result that Bent



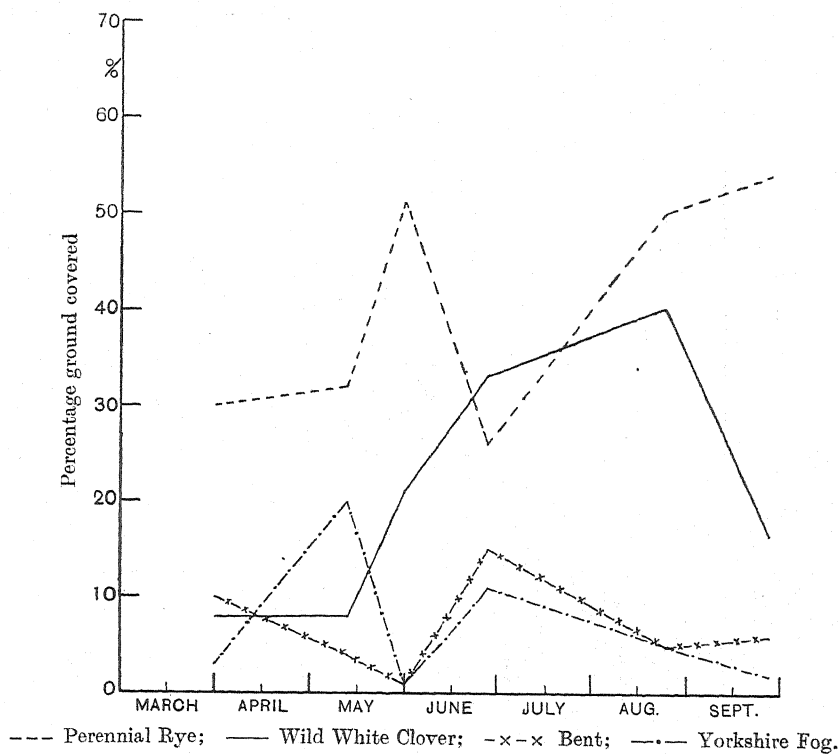
and Yorkshire Fog are still further depressed, and that Wild White Clover and Rye Grass are greatly increased. It was also evident that the quality of the herbage in B was superior to that of A, and consequently more nutritious, so that the closer grazing had not merely improved the botanical but in all probability the chemical composition (12).

The botanical composition of the old herbage as judged by the condition of both East Down and Knight's-Hayes is quite in keeping with some of

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was beginning vigorous growth, and the after-treatment did everything to favour Bent. Hence, in the course of a few years, Bent was the dominant or one of the dominant grasses. Under good grazing and manuring the conditions are so improved that the better grasses and clovers are able to compete with such plants as Bent, Yorkshire Fog, Soft Brome and weeds in general.

It will be seen from Graphs I-VII that Yorkshire Fog and Perennial Rye affect each other. When Rye is in high proportion Yorkshire Fog is at a low figure. Both tend to have two peaks of maximum development during the



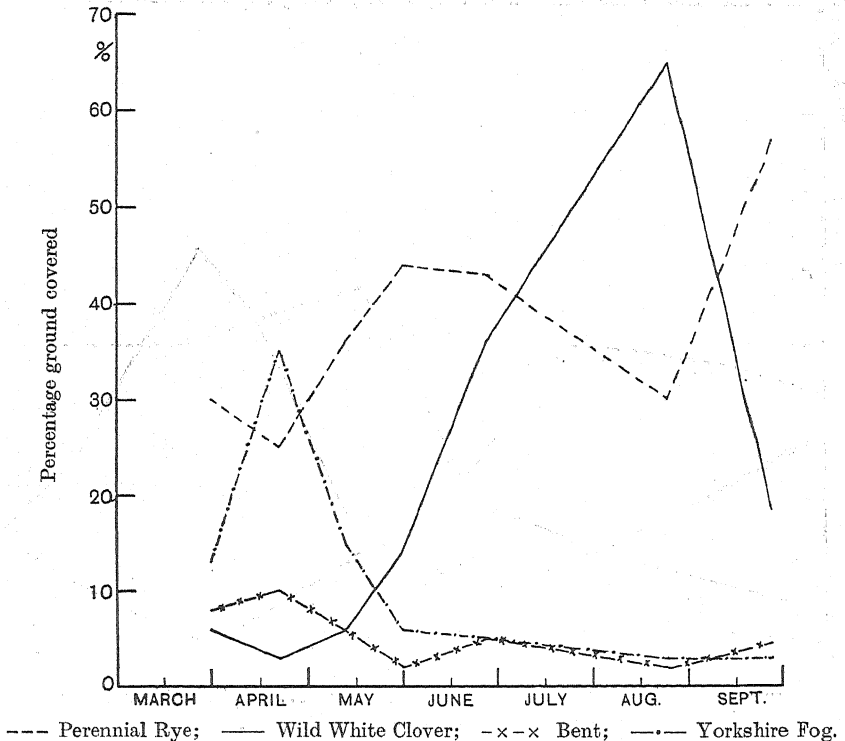
Graph III, Plot 3. Knight's-Hayes, 1927.

year. Yorkshire Fog just reaches its maximum area of ground covered in April, and the next period, depending on competition, is June to August. In some cases there is no second fluctuation. Perennial Rye reaches its final peak of development in May and the second and larger increase is towards September and October, although in Plot 3 the curve showed a tendency to fall.

Perennial Rye Grass and Wild White Clover, which form a very important association in well-grazed grasslands in good condition (1), also show a fluctuating movement. Whenever Perennial Rye is at a peak in the curve Wild White Clover is at a depression, especially where grazing is adequate. On the other hand, in moist growing weather, if the grass is not kept down, Wild

White Clover does get depressed but recovers very rapidly as soon as the grass is adequately grazed.

If the curves of Yorkshire Fog and Wild White Clover are compared, it will be seen that when Yorkshire Fog reaches a high peak about April-May, Wild White Clover shows a depression in its curve of growth. Although Wild White Clover shows a marked fall again towards the end of the year, which the slight increase of Yorkshire Fog and Bent would not explain, it is easily explained by the high proportion of ground covered by Perennial Rye, as a result of



Graph IV, Plot 4. Knight's-Hayes, 1927.

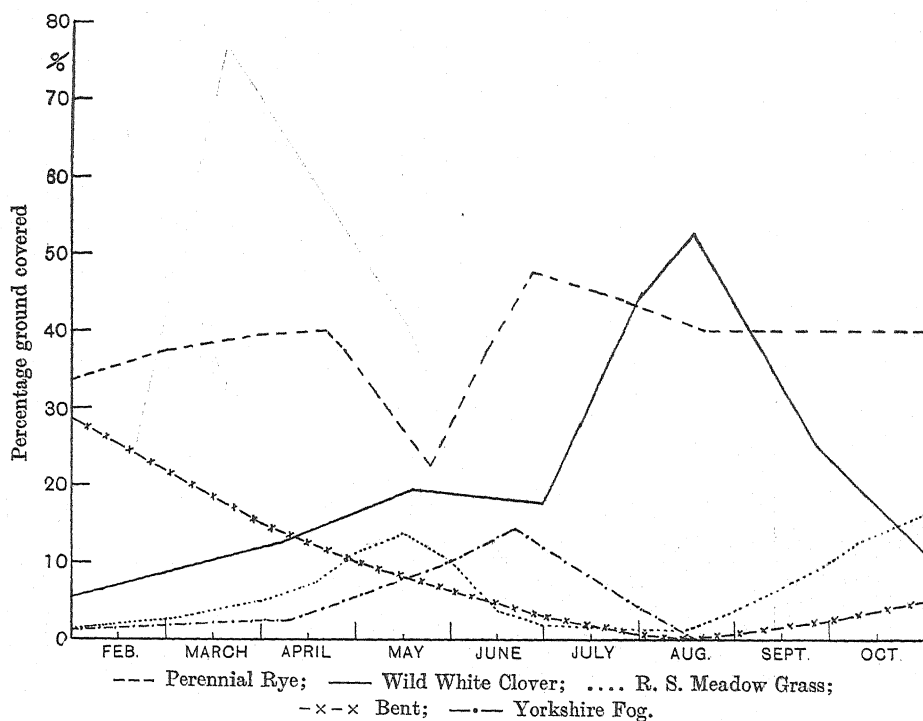
the good condition of the soil aided by Wild White Clover. This is brought out by the percentage of crude protein in samples of mixed herbage from all plots (Knight's-Hayes); April, 21 per cent.; May, 21 per cent.; June, 19 per cent.; July, 22 per cent.; August, 26 per cent.; September, 27 per cent.<sup>1</sup> Bent tended to increase from June to July and again towards the end of September. It never succeeded, however, in making any serious headway against the Rye Grass-Wild White Clover association. Plots 3, 4 and 5 in East Down had Bent in rather higher proportion.

<sup>1</sup> Figures kindly supplied by Mr A. Blenkinsop, B.Sc.



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Knight's-Hayes showed a strong similarity to East Down in floral fluctuations and changes. Weeds as distinct from miscellaneous plants were few, and it was readily seen that in Knight's-Hayes they had been carried along the water channels and distributed from there. This distribution, therefore, had occurred during the previous years when the field was a water meadow. The distribution of weeds along the water channels is a very marked feature of many water meadows in the south-west. It will be noted that moss shows no tendency to occupy the high proportion it did during the early part of the year. The fact that there was very little, if any, space bare of vegetation



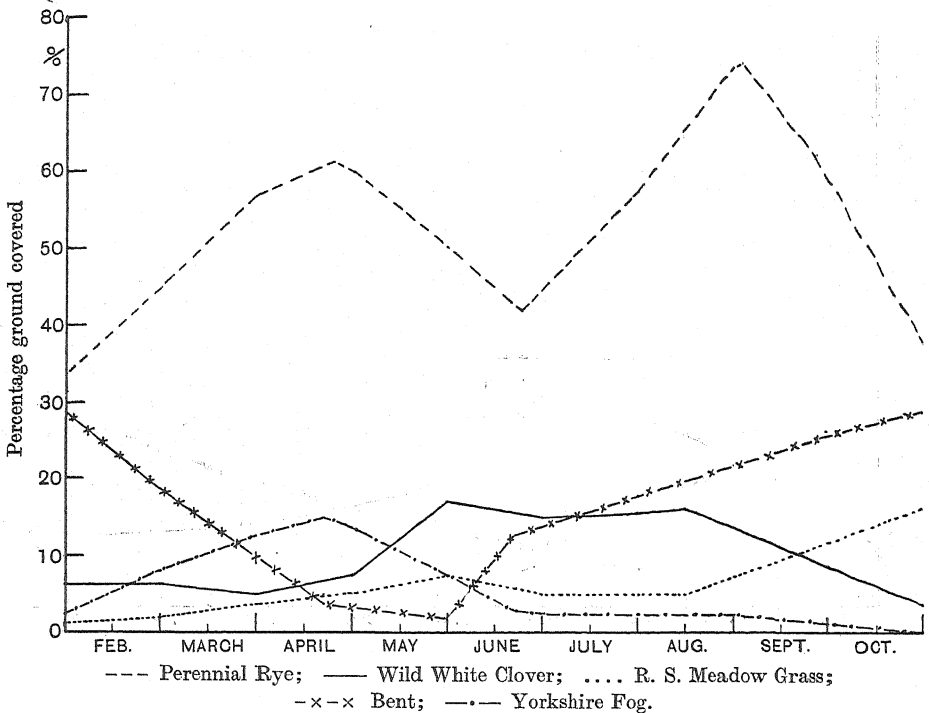
Graph V, Plot 1. East Down, 1927.

(beyond turf cut up by treading in wet weather) prevented moss making any progress. Grazing did not favour Meadow Foxtail, and by September there was scarcely a plant to be seen.

The effect of the grazing and manurial treatment was interesting in several species. Yorkshire Fog, as already pointed out, was not grazed at first. Later, as the effects of the manure became more evident, it was well grazed and it consequently decreased. Bent was almost similar in that stock did not favour it much, but later, when it did grow it was eaten, though not with the same readiness as Rye Grass and Clover. Another point was that grazing tended to pull it up and prevent spreading. This is an important point, for pastures

on heavy soil where Bent is prevalent if rolled injudiciously (depending on condition of soil when rolling and the amount of rolling) may get dominated by Bent.

The presence of Sorrel (*Rumex Acetosa*) at Knight's-Hayes was due partly to the previous poor condition of the soil, and partly to the fact that seeds had been washed along the water channels and thus spread over the field. At the side of one of the water channels in Plot 4 there was some *Polygonum Persicaria*, but no trace of it elsewhere. There were small quantities of *Ranunculus repens*, *Bellis perennis*, and latterly of Hawkweeds (*Hieracium* spp. and *Hypochaeris radicata*).



Graph VI, Plot 4, East Down, 1927.

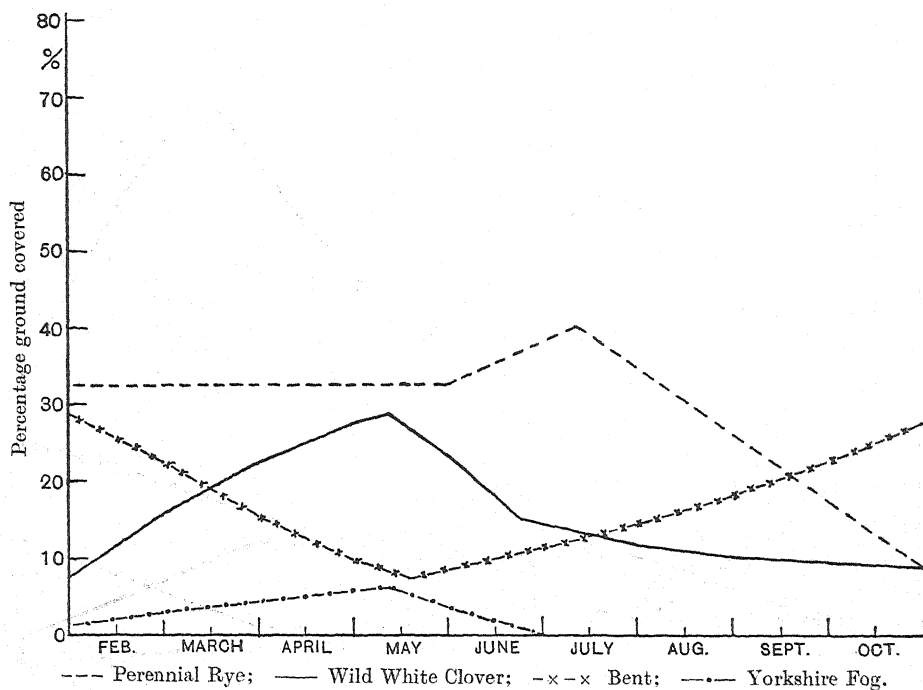
The copious autumn rains made growth so profuse that it was with great difficulty that the herbage was held in check. This was the chief cause of Perennial Rye Grass reaching such a high figure towards the end of the observations. Weeds in East Down were not plentiful, if Buttercups are excluded. Daisies were practically absent, but Soft Brome and Golden Oat Grass were both present in the early stages.

The marked improvement in the vegetation as a result of manuring and grazing is not only evident in the figures, but the well fed and sleek appearance of the stock as well as the market prices was inclusive evidence. It was

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perhaps more evident at Knight's-Hayes than at East Down, since the latter suffered from severe drought. Even in spite of this the results were very satisfactory. The final condition of the vegetation as judged by the figures bore a strong resemblance to that of some of the best fattening pastures as shown by Armstrong (1). This is a good indication that the sectional grazing and manuring method is on the right lines.

The difference between percentage of ground covered and the "young hay" or green growth 8-10 in. high as estimated by weight is not so great as the figures suggest (Tables I and II). The taller growth favoured certain plants



Graph VII, Control B, East Down.

and presented growth in height which grazing did not. This favoured the tall growing at the expense of a creeping plant like Wild White Clover and Rye "grew up" rather than "spread out." Many weeds are also encouraged by the longer growth and seem to be more plentiful in hay.

An important point is very clearly illustrated in Graph VII for the control area in East Down. It will be seen that Wild White Clover and especially Perennial Rye were late and slow in making spring growth. Not till May was any real progress made. In both Plots 1 and 4 (as examples of the five plots) Wild White Clover and Perennial Rye made growth from a very early stage. It is also evident that Bent again virtually gained a position of dominance at the close of the year. This smothering influence of Bent at the beginning

and end of the growing season is one of the worst features of many pastures. Its decaying stems and leaves act in every sense of the word as a "cold blanket" on early spring growth. In the various plots it will be seen that Bent was successfully dominated by Rye Grass. In Plot 1 (Graph V), East Down, Perennial Rye and Wild White Clover had most successfully crushed Bent. This means that good grazing is available till very late in the year. In other words the productive season of growth is considerably lengthened, first by a much earlier start, and secondly by a much lengthened growing period. When the weather becomes colder, Wild White Clover slows down its growth as is shown by the curves in all graphs, while Perennial Rye continues to grow though more slowly throughout the year in most of the south Devon districts. The five plots at East Down fall into two groups. Plots 1 and 2 were practically similar in flora, while Plots 3, 4 and 5 illustrate rather a different state of affairs. Wild White Clover is not so prominent in Plots 3, 4 and 5, owing to slight stocking difficulties in the early stages of growth. The drought took greater effect on the surface of the ground and adversely affected Plots 3, 4 and 5. The proportion of Bent is also somewhat higher, but another season will bring these plots into line with 1 and 2. The chief difference was that Plots 3, 4 and 5 had a very high proportion of Rye, while 1 and 2 had a higher proportion of Wild White Clover.

The figures in Knight's-Hayes and East Down show very clearly that the continuous and regular manurial and grazing treatment had changed the rather varied vegetation into a homogeneous Rye Grass-Wild White Clover association very typical of some of the very best pastures, and in particular to some of the very rich, irrigated areas, known as Lord's Meadows at Crediton (Devon). There, on alluvial and fertile soil, the periodic flushing of the old pasture land (divided into plots) by the effluent from the town sewage has led to the formation of a very homogeneous flora. An examination of the plots (each several acres in extent) gave the following analysis: Wild White Clover, 20; Rye, 45; Rough Stalked Meadow Grass, 7.5; Meadow Foxtail, 0.5; Crested Dogtail, 1; Bent, 15; Yorkshire Fog, 10; Cocksfoot, trace; Buttercups, 5.

The analysis was made on June 27th, 1927. It will be seen that there is a very marked resemblance between the figures for Crediton and those for Knight's-Hayes and East Down. In both cases Bent and Yorkshire Fog were the only two prominent species after Rye Grass and Wild White Clover. Rough Stalked Meadow Grass is higher at Crediton owing to the periodic flushing. It is evident, therefore, that the manurial treatment of the plots at Knight's-Hayes and East Down (allowing for grazing being equivalent in all places, which from observation seems to be a fairly reasonable estimate) is equivalent to the flushing of meadow land with the effluent from a town's sewage as far as the botanical side of the question is concerned. One plot in the centre of this area was easily picked out, owing to the difference in colour of the vegetation and the fact that the stock were not grazing. On investigation it was

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found that the vegetation consisted of 90 per cent. Bent, the remaining 10 per cent. consisting of a little Perennial Rye, Yorkshire Fog, traces of Meadow Grass, Buttercups and an occasional plant of Wild White Clover. The grazing (or lack of it) had been inadequate; since all other factors were the same for this plot as the others, it brings out very clearly the vital importance of management. Where the fences separated this plot from the others there was a sharp line of demarcation. The surrounding plots had a fresh and plentiful growth, while the Bent plot had practically no keep and was very stemmy. Incidentally this raises the question why the effluent of many inland towns is not used in this way. The manurial value of the effluent is high, and in too many cases it is either not used to the best advantage or wasted. That the regular application of sulphate of ammonia to grassland (other things being equal) produces the same result speaks well for this manurial treatment. It suggests that where such irrigation methods are not possible or available the same or equivalent results may be achieved by skilful treatment and manuring.

Without going into agricultural details there are two points which affect the botanical side. The problem of adequate and even spreading of the dung is important. The plots at Knight's-Hayes were harrowed with a chain harrow, but this was not always too successful. A parimeter harrow would help matters (or a flexible type as used at Seale-Hayne). Where the droppings of cattle fall and are left not properly distributed, tufts of deep green vegetation spring up which stock refuse to eat for some time. These tufts tend to become coarse, to upset the vegetation, and make it patchy, and may affect the health of the grasses (5).

The other point is the application and spreading of sulphate of ammonia. The application of this manure tends to scorch the vegetation slightly, and Wild White Clover chiefly suffers. Where grasslands tend to become scorched the application of sulphate of ammonia may produce unexpected results, such as "burning" the Clover. Where possible and practicable sulphate of ammonia should be applied in dull or even wet weather. This mitigates or obviates the scorching danger. A bright dry sunny day should be avoided where possible or the clovers are bound to suffer. It is obvious that it is not always practicable or possible to follow such suggestions, but where they can be put into force it will make a considerable difference by the end of the year, not only in the quantity but in the quality of the herbage. This scorching is often compensated for by the scorching of the leaves of any weeds present. The question arises, however, whether two lighter dressings (half quantity each time) with a brief interval between might mitigate, if not remove, this trouble.

The question of the effect of nitrogenous manures on leguminous plants, especially clovers, is always an important one. It was for long considered wrong to use anything like sulphate of ammonia on grassland as the Clover would be depressed. This is generally true, since the application of this manure alone (with no lime) tends to increase the acidity of the soil, and consequently

make it less suitable for plants like Wild White Clover. It also stimulated grasses and tall growing plants which were often not adequately grazed, with the result that Clover was overshadowed, decreased, and might almost disappear. Where sulphate of ammonia and other nitrogenous manures were applied to grassland in the past, a whole field was treated. The result was a vigorous growth of vegetation which was not properly grazed, as the stock was often insufficient to graze the area evenly. Selective undergrazing soon made the vegetation worse than it previously was. The field became half hay, half pasture, with numerous coarse tufts of growth no stock would touch, and many deep-rooted weeds were often present. Had a half or a third of the area been treated the result might have been very different. Naturally the slower method of phosphatic manuring was more successful, since the improvement in the leguminous growth gradually assisted the grasses. It was a slow steady improvement, not a sudden flash of growth, and there was in consequence no stocking difficulty.

That the application of nitrogenous manures to clovers is not necessarily harmful is easily demonstrated. If Crimson Clover is grown in culture solution the first plants to suffer are those with no nitrogen. Not only so but in late, cold and backward seasons, some farmers top dress Crimson Clover<sup>1</sup> with sulphate of ammonia with very good results. The factor which affects many legumes is acidity, as this seems to affect the root nodule bacteria retarding or inhibiting the nitrogen supply. Potash and phosphates also play an important part, not only as far as the plant itself is concerned, but also affecting the bacteria in the nodules. An application of farmyard manure to some old pastures produces wonderful results. Not only is Wild White much improved, but even Wild Red Clover may appear to a considerable extent. It is obvious, therefore, that it is not the application of nitrogenous manures which causes the decrease or disappearance of clovers in pastures. It is secondary results such as increase of acidity, unbalanced manuring, or unduly increasing nitrogen out of all proportion to other necessary plant foods that cause the trouble. In fact, the only damage likely to occur is the danger of scorching the leaves of Wild White Clover with sulphate of ammonia in dry, sunny weather. Even this may be only a temporary setback and almost balanced by the damage due to surface growing weeds. Hence, provided the nitrogenous material is balanced by other things necessary, and that the grazing is adequate and well managed, clovers instead of being depressed are stimulated, since their roots absorb nitrogen from the soil like those of grasses and other plants. Even in 1886 Hillriegel and Wilfarth demonstrated with peas the necessity of nitrogen in sterilised sand and that growth of these plants under such conditions was quite comparable with oats and barley (7).

It was unfortunately impossible to get sample analysis of vegetation by weight (Table II). The "hay" analysis is a phase beyond the grazing stage,

<sup>1</sup> *Trifolium incarnatum*.



and cannot be closely compared with the percentage ground covered method. Cutting does not quite represent grazing, so that a close comparison is not possible. The figures in Table II are interesting, as they indicate what might happen if grazing is not skilfully managed. The tables also give an interesting glimpse of the effect of this treatment on the various plants of the pasture from the point of view of hay production. In this respect there is some tendency towards what has already been recorded by Somerville (9), and by Dr Brenchley in *Manuring Grassland for Hay* (Rothamsted Monographs).

It is evident from Diagram 4 (Plot 1, 1929) that there has been little change in the vegetation of East Devon under the system of controlled grazing and manuring. Since the close of 1927, when the older and more heterogeneous flora had altered to a flora of fewer species and of a much more homogeneous nature, the dominating species had not changed. Fluctuations were evident in Yorkshire Fog and Bent, slight increase in weeds and miscellaneous plants, while Crested Dogstail and Sweet Vernal had disappeared. Weeds consisted of *Ranunculus*, *Plantago*, and *Bellis perennis*, and of these perhaps *Plantago lanceolata* is not entirely a weed if present in small quantities. Hence, beyond seasonal fluctuations, so long as the method of treatment does not vary, the flora of the grassland remains practically constant from year to year.

#### SUMMARY.

The effect of sectional grazing combined with adequate manurial treatment not only increases the stock-carrying capacity of the vegetation (yield), but increases and prolongs the vegetative period of growth.

The nature of the vegetation alters in the proportion of the various plants present while the number of species tends to decrease.

The outstanding differences are the marked increase of Perennial Rye Grass and Wild White Clover which under good treatment tend to form an association.

This association of Perennial Rye Grass and Wild White Clover (and sometimes Rough Stalked Meadow Grass) dominates Bent, Yorkshire Fog and weeds, so long as the soil remains in good heart and the grazing is skilfully managed.

If growth is allowed to become longer than is necessary for rotational grazing, certain grasses and weeds are afforded a greater opportunity. This is evident for Meadow Foxtail, Cocksfoot, Rough Stalked Meadow Grass, Bent, Yorkshire Fog, and weeds in the fenced plots. Even Crested Dogstail and Sweet Vernal increase when near the flowering stage.

Judging from the present investigation it seems that applications of such manures as sulphate of ammonia following a general treatment can, with judicious grazing, produce the same result as irrigation with the effluent of

town sewage. The resulting vegetation in both cases shows a strong resemblance to the flora of fattening pastures.

Unless the grazing and management of the plots are carefully handled, the result may be very adverse, since weeds might be unduly encouraged. The proportion of weeds present in some of the "hay" samples indicate this tendency. The one poor plot on Lord's Meadows clearly indicates the vital importance of management of both grassland and stock.

The very marked improvement in the vegetation of grassland under a system of manuring and sectional grazing as dealt with, is due to two factors: (1) carefully controlled grazing, and (2) judicious manuring.

The effect of sulphate of ammonia and other nitrogenous manures is not directly depressing on Wild White Clover, provided there is no deficiency in lime, phosphate and potash, and that grazing is carefully controlled. In dry weather sulphate of ammonia may scorch the leaves of Wild White Clover, but any injury caused is neither serious nor permanent.

Apart from slight seasonal fluctuations, after the initial changes have occurred in the flora of grassland under any method of controlled treatment, the *status quo* of the various species will not alter so long as the treatment remains constant.

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# ON THE IMPORTANCE OF SOME MOSSES AS PIONEERS ON UNSTABLE SOILS

By W. LEACH.

(With Plates VIII and IX.)

THE occurrence of such mosses as *Polytrichum piliferum*, *P. juniperinum*, and *Ceratodon purpureus* as pioneers on various types of soil in this country, is well known to ecologists. In ecological literature we repeatedly find these species mentioned as being the first colonisers of sand in secondary seres on inland sandy regions, and also on heath-land where burning of the *Calluna* has taken place. Further, we frequently find *P. piliferum* and *P. alpinum* acting as pioneer species on certain types of rock detritus. There does not appear to have been carried out, however, any critical examination of the reaction of these plants on the soil. It is therefore proposed to describe here some observations which throw light on this question.

Of the species mentioned above, *P. piliferum* is the most widespread in its distribution in the British Isles. It occurs as a pioneer on non-calcareous soils of compositions varying between moderately fine rock detritus or gravel, and sandy clay.

## PIONEER STAGES ON ROCK DETRITUS.

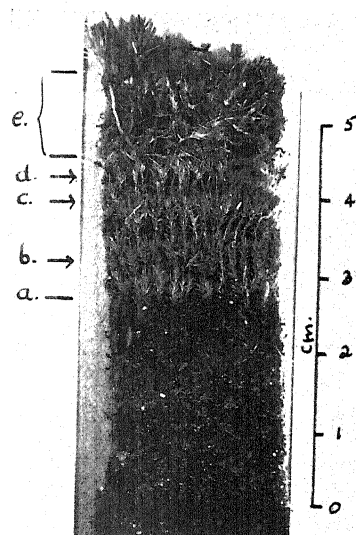
In exposed situations, e.g. hill-tops up to about 2000 ft. (600 m.) above sea level, where the rock is soft and weathers down to fragments of round about 1 or 2 cm. in diameter, *P. piliferum* is often an important agent in the stabilisation of the substratum, and the initiation of re-colonisation. In such positions, patches of vegetation are often removed by weather action, thus giving rise to bare areas on which re-colonisation may begin. Pl. VIII, phot. 1, shows such an area on the summit of Caer Caradoc in Shropshire at an altitude of 1500 ft. (450 m.). Denuded areas of this nature are frequently to be found

## EXPLANATION OF PLATE VIII.

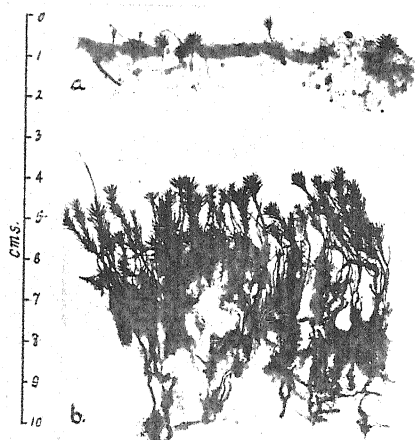
- Phot. 1. Denuded area of detritus on summit of Caer Caradoc with *Polytrichum piliferum* as a pioneer recolonising species.
- Phot. 2. Sections through open (*a*, above) and closed (*b*, below) communities of *P. piliferum* on pure sand from Prees Heath. For description see text.
- Phot. 3. Upper section shown in Phot. 2, after washing away sand layer.
- Phot. 4. Washed sections of open (*a*, above) and closed (*b*, below) communities of *P. piliferum* on pure sand. For description see text.
- Phot. 5. Washed section through moss turf developed after burning of *Calluna*. *a*, *b*, *c*, *d*: successive communities of *Ceratodon purpureus*; *e*: *P. piliferum* and *Webera nutans*. For description see text.



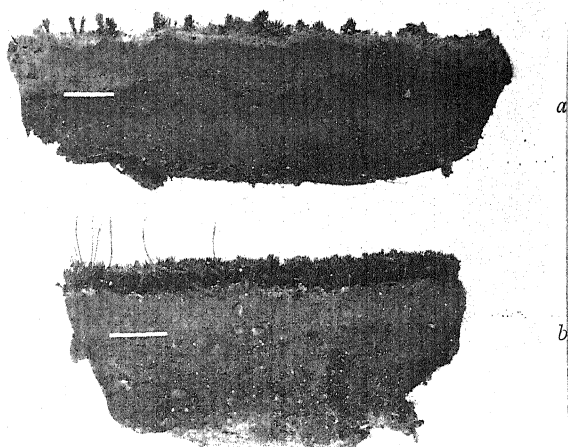
Phot. 1.



Phot. 5.



Phot. 4.



Phot. 2.



Phot. 3.



showing various stages in the process of re-colonisation, and *P. piliferum* usually occurs as a pioneer. The early appearance of the *Polytrichum* is often due, to a considerable extent, to vegetative growth of small fragments of the moss that become lodged between the stones. These fragments become anchored to the substratum by rhizoids, and send up new leafy shoots. A sparsely arranged group of *Polytrichum* shoots on such a patch of detritus will be found, on examination, to possess a far more extensive underground system of stems and rhizoids than its appearance above ground suggests. The binding action of the rhizoids upon the fine soil between the stones, and actually upon the stones themselves, becomes evident if we try to free the moss from the soil by washing. The efficacy of the rhizoids of species of *Polytrichum* in this capacity is increased by their frequent aggregation into complex "wicks." Species of *Polytrichum* differ from the majority of other mosses in their ability to produce long underground stems, which turn brown and are remarkably tough and strong. This ability to form rhizome-like shoots is mainly due to the fact that the photosynthetic activities of these species are sufficient to provide a food reserve which enables them to grow for long periods in absence of light (2). We thus find that they are not killed, even when buried to very considerable depths, as often occurs in exposed situations, owing to movements of rock fragments and soil by weather action. When this happens, new shoots grow out which branch freely, and usually eventually reach the surface. Also from these underground shoots numerous soil-binding rhizoids spring.

Above altitudes of 2000 ft. (600 m.) the place of *P. piliferum* on rock detritus of the type described above is, in this country, taken by *P. alpinum*. Pioneer colonisation by this latter species may often be seen on exposed mountain tops where the typical climax vegetation is frequently a *Rhacomitrium lanuginosum* community. The *Rhacomitrium* grows over the surface of the detritus and forms a protective carpet against weather action, but its rhizoids have no very great soil-binding effect. Patches of this *Rhacomitrium* carpet are frequently destroyed by the action of weather, and *P. alpinum* takes on the rôle of pioneer, and stabiliser of the detritus, just as *P. piliferum* does at lower altitudes.

#### PIONEER STAGES ON SAND.

It is as pioneers on sand that *P. piliferum* and *P. juniperinum* are able to exercise their soil-binding qualities most effectively. As a consequence, these species may often be of considerable importance on heath-land occurring on sandy soils. On such areas in the midlands and south of England, owing to the operation of various biotic factors such as human interference and rabbit burrowing, patches of the heath vegetation are often destroyed. In this way exposures of what is often practically pure sand are formed, and in dry windy weather this sand is freely blown about. We find *P. piliferum* mentioned by Farrow (1) as a coloniser of bare sand in Breckland, but no attention is drawn



by that author to the particular features possessed by the moss, which specially fit it for this rôle.

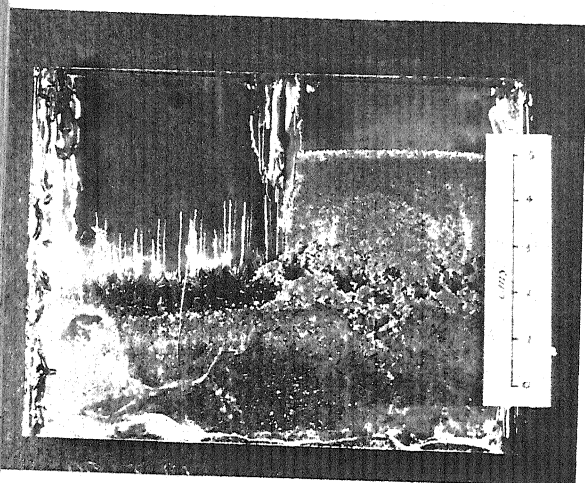
In the course of examining similar colonisation of sand by *P. piliferum* and *P. juniperinum* at Hartlebury Common in Worcestershire, Prees Heath in Shropshire, Bickerton in Cheshire, and other localities in the midlands, it seemed probable that some information regarding the moss succession might be gleaned by washing away the sand from sections cut through the areas undergoing re-colonisation. Rectangular blocks of the sand, on which moss communities were growing, about 10 cm. square in surface area and 5 cm. to 10 cm. thick, were carefully cut round with a knife, and dug up. These were taken into the laboratory, and cut into vertical slices about 0.5 cm. to 1 cm. in thickness. These slices were then laid on a sheet of glass, and a fine jet of water was directed on to the cut surface, so that the soil was washed away from the underground moss stems.

Pl. VIII, Phot. 2, shows sections cut through blocks of soil bearing open and closed communities of *P. piliferum* from Prees Heath. It will be seen that, in the case of both of these communities, the soil consists of a layer of blown sand overlying the original heath-peat, the junction between the two layers being indicated on the photographs by white lines; the original vegetation which grew directly on the peat having been destroyed by fire before the sand was deposited. Pl. VIII, Phot. 3, shows part of the section through the open community (marked *a* in Phot. 2) after washing away the sand layer with a jet of water. Several shoots of the original *Polytrichum* community that appeared on the peat surface after burning can now be seen in this section, as the sand which covered them has been removed. It can also be seen how a renewed apical growth of these shoots has resulted in the persistence of the *Polytrichum* community in spite of its having been covered with the sand. Another point of interest brought out by this treatment of the section is the fact that the presence of the sand covering apparently induces an abundant development of rhizoids on these new apical shoots, and also causes prolific branching.

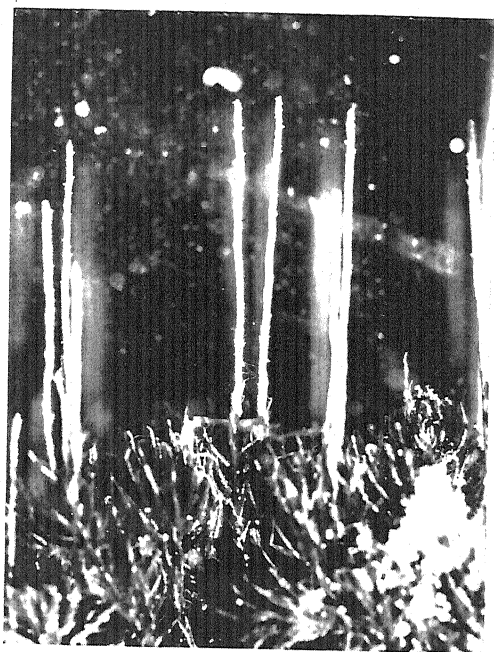
We thus find that the covering of an open *P. piliferum* community by a layer of sand results in its progression from the open to the closed state, and at the same time the sand layer becomes effectively bound together and stabilised by a dense system of moss rhizoids.

Some idea of the possible extent to which this raising of the soil level by blown sand stabilised by *P. piliferum* may proceed, is indicated by the fact that sections cut through deep sand bearing a closed community of this moss, from Hartlebury Common, showed living shoots of the moss going down to depths of more than 20 cm. Also at various depths below the surface were found small, dead plants of *Festuca ovina*, a fact which shows that this grass is not always able to cope with sand accumulation by sending up new shoots, as described by Farrow (1).

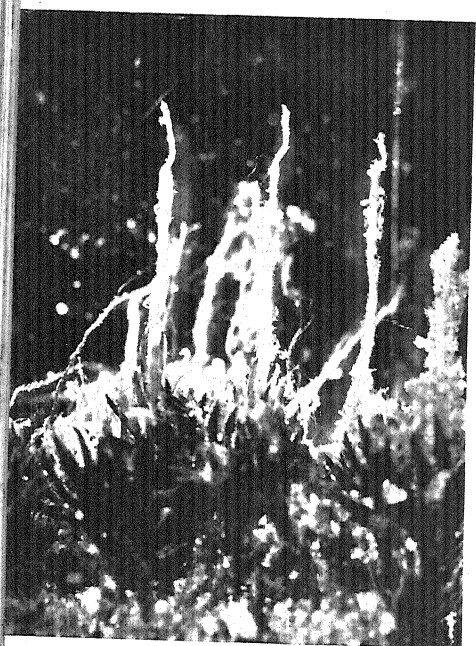




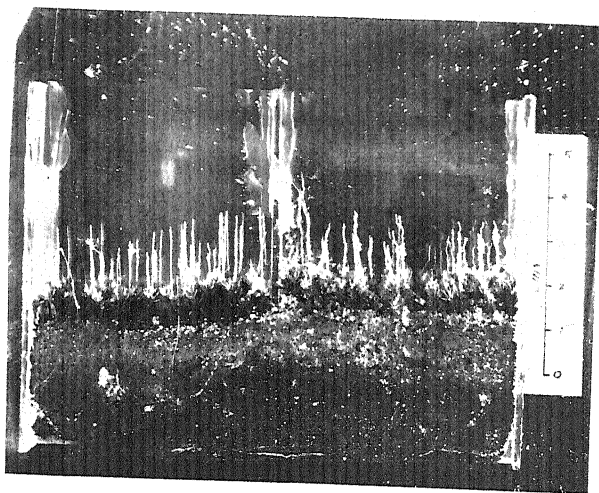
Phot. 6. Experiment set up to demonstrate the effect of a layer of sand on a community of *Polytrichum piliferum*. For further description see text.



Phot. 8. Enlarged view of etiolated *Polytrichum* shoots shown in Phot. 6, which were developed in darkness on the moss not covered with sand.



Phot. 9. Similar to Phot. 8, but showing etiolated shoots developed on the moss which was covered with sand. Note presence of numerous rhizoids on the etiolated shoots.



Phot. 7. Same experiment as shown in Phot. 6, after removal of sand.

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Pl. VIII, Phot. 4 shows washed sections of open and closed *P. piliferum* communities from Prees, taken from an area where no layer of peat was present below the sand. In the case of the open community (marked *a*), the moss colonisation appears to have arisen from a recent germination of spores and formation of protonema. This section shows how, even in the early stages of colonisation, a very effective stabilisation of the surface layers of the sand is brought about by an extraordinarily abundant growth of rhizoids. Thus the soil-binding effect of the moss becomes important, even in the early stages of the colonisation.

This washing method will often be found to yield interesting information regarding moss successions. Pl. VIII, Phot. 5; shows a section through a moss turf from Maiden Castle in Cheshire, taken from an area where *Calluna* had been burnt some years previously. Here the dominant species, forming a closed community on the surface, were *P. juniperinum* and *Webera nutans*. Subsequent to the destruction of the *Calluna*, it will be seen that four communities (marked *a*, *b*, *c*, and *d* in Pl. VIII, Phot. 5) of *Ceratodon purpureus* have developed on the site. Each of these communities was covered in turn by a layer of blown sand, through which the moss shoots grew and re-established themselves. Finally the composition of the moss community changed from pure *Ceratodon* to the mixture of *Polytrichum juniperinum* and *Webera nutans* which existed on the surface at the time when the examination was carried out (layer *e*, Pl. VIII, Phot. 5). A point of interest is that the *P. juniperinum* shoots could be traced right down to the peat layer, which suggests that this species had developed either vegetatively from a few shoots that had survived the burning, or from spores that germinated on the area shortly after the burning occurred. The presence of these clear-cut moss layers in the section is obviously due to an alternation of dry periods during which sand was deposited, with damp or wet periods during which the moss grew normally. The actual duration of these periods could not, unfortunately, be discovered.

In order to obtain definite information as to the actual effect of the presence of a layer of sand over a *P. piliferum* community, the experiment shown in Pl. IX, Phot. 6, was set up. A section about 1 cm. thick of the soil bearing a closed moss community was cut out as described above, and enclosed between glass plates. Half of the moss-covered surface was then covered with a layer of sand about 2.5 cm. thick as shown, the other half being left uncovered. The whole was then placed in darkness and kept moist in the laboratory. Three months later the sand which had covered half of the moss shoots for the period of the experiment, was removed by washing. Pl. IX, Phot. 7, shows the appearance of the *Polytrichum* at the end of the experiment. It will be seen that, during the experiment, the leafy shoots of the moss have grown out into long etiolated stems bearing minute scale-leaves. While the etiolated shoots that developed in air (the left-hand half of the experiment in Phot. 6) are straight, smooth, and unbranched, those that had developed in the sand

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layer are sinuous and frequently branched, and have produced a considerable growth of rhizoids to which in a number of places, sand grains have remained firmly attached. Pl. IX, Photos. 8 and 9, give magnified views of these two sets of etiolated shoots, and clearly show how the presence of the sand increases branching and rhizoid production.

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# INTERNATIONALE VEGETATIONSKARTE EUROPAS UND VORSCHLÄGE FÜR EINE INTERNATIONALE FARBEN- UND ZEICHENGEBUNG

## VORTRAG GEHALTEN AM INTERN. BOTANISCHER KONGRESS IN CAMBRIDGE

VON H. BROCKMANN-JEROSCH, *Zürich.*

MAN kann sagen, dass die Soziologie in den letzten 30 Jahren sich zu einem Achtung gebietenden Zweig der Pflanzengeographie entwickelt hat. Was hier mit viel Kraft und Energie erreicht wurde, gehört zu dem Besten und zum unbestrittenen Gebiet der neueren pflanzengeographischen Leistungen.

In einem ersten Zeitabschnitt standen die Karten im Vordergrund, die die ganze Erde umfassen, ein Inventar der Kenntnisse darstellen, wie es Grisebach in seiner immer noch so lesenswerten Vegetation der Erde<sup>1</sup> angestrebt hatte. Auf seiner Karte der Vegetationsgebiete der Erde fussen wohl alle späteren, so die wichtigste der damaligen Zeit, diejenige von Drude<sup>2</sup>. Sie wurde mehrfach umgearbeitet, aber in den Grundzügen konnte diese klassische Karte bestehen bleiben. Drude fand später den Zeitpunkt für gekommen, weiter zu gehen. Auf dem internationalen Geographenkongress von 1899 in Berlin legte er kartographische Darstellungen von Pflanzengesellschaften, die bereits schon viele Einzelheiten umfassten, und noch eingehendere 1905 in Wien vor<sup>3</sup>. Aus diesen Vorschlägen heraus wuchs nun eine neue Art von Karten; sie umfassen kleine, ausgelesene Gebiete, gehen dafür aber bereits in viele Einzelheiten.

Durch den grossen Einfluss von Schimper und Warming auf die Pflanzengeographie erhielt die physiologische Seite einen ungeahnten Aufschwung. Das zeigt sich auch in der pflanzengeographischen Kartographie. Überall wird Vertiefung gesucht und die ökologische Seite wird verfeinert. Zugleich nehmen immer neue Nationen, nach und nach fast alle Kulturvölker, an dieser Arbeit teil.

Die Auswahl der Gebiete geschieht aber immer nach recht persönlichen Gesichtspunkten. Dass der Pflanzengeograph möglichst die natürliche Vegetation zum Studium erwählt und dabei Stellen sucht, wo sie grossem Wechsel unterliegt, kann ihm niemand verübeln. Solche Vegetationen findet er im Gebirge, am Ufer der Seen und ähnlichen Orten vor, sodass diese Gebiete besser bearbeitet sind als diejenigen, die stark unter dem Einfluss der Menschen stehen.

<sup>1</sup> GRISEBACH, A. *Die Vegetation der Erde nach ihrer klimatischen Anordnung*, Bd 2. Leipzig, 1872. Masstab 1 : 135,000,000

<sup>2</sup> DRUDE, OSCAR. "Vegetationszonen der Erde." *Berghaus physikalischer Atlas*. Gotha, 1887. Masstab 1 : 100,000,000.

<sup>3</sup> Weinböhla, Tschirnsteine und Altenberg wurden als Beispiele veröffentlicht in Engler's *Bot. Jahrbücher*, Bd 40, Beibl. 93, S. 10, 1908.



Die immer eingehenderen Karten hatten natürlich eine gute kartographische Unterlage und zugleich äusserst ausgearbeitete Methoden zur Voraussetzung. Was für prächtige Karten vorhanden sind, was sie alles bieten, die Vielseitigkeit der kartographischen Gesichtspunkte und die Art der Darstellung zeigte schon Schröter 1910 am 3. internationalen Botaniker Kongress in Brüssel<sup>1</sup>. Und doch: unter diesen vielen neuen Karten ist nicht eine, die versucht hätte, die Pflanzengesellschaften Europas insgesamt darzustellen. Wieder müssen wir hier auf Drude zurückgehen, der im Berghaus-Atlas die eingehendste Darstellung gegeben hat. Diese Karte stammt aber aus dem Jahre 1887 und ist in kleinem Masstabe gehalten.

Wenn wir bedenken, dass wir aus Europa die meisten pflanzengeographischen Karten und Studien besitzen, dass die europäischen Gebirge die am besten untersuchten sind, so zeigt das sehr deutlich den grossen Widerspruch und das wird den Aussenstehenden, hauptsächlich den Geographen erstaunen.

Durch diese Zurückhaltung sind wir nun so weit gekommen, dass die Darstellung der Vegetation von Afrika, des dunklen Erdteiles, weiter gediehen ist als diejenige Europas. Auch die Vereinigten Staaten haben ihre prächtige Vegetationskarte, die uns soeben Kollege Shantz vorgeführt hat und um die wir ihn fast beneiden möchten. Bei uns bleiben einzelne sehr genau bearbeitete Gebiete isoliert, ohne Zusammenhang untereinander.

Derjenige, der im Stoffe selbst aufgewachsen ist, kennt die vielen wichtigen Schlüsse, die sich aus Übersichtskarten ergeben, und es bleibt von ihnen fast kein Gebiet der biologischen und geographischen Wissenschaft unberührt. Die Zusammenhänge zwischen Klima und Vegetation zeigen sich vor allem in den grossen Zügen der Pflanzenverbreitung, insbesondere aber im Vorherrschen gewisser Lebensformen und Arten, was wiederum in der Zusammensetzung der Pflanzengesellschaften seinen Ausdruck findet. Die Pflanzendecke selbst stellt die Bodenverhältnisse dar und diese sind das Ergebnis der geologischen Unterlage und der Art der Verwitterung und Bodenbildung. Die Bodenproduktion beruht bei primitiver Kulturstufe, so bei Sammlern und Hirten auf der natürlichen Vegetation. Gewiss haben wir von solchen Gebieten nicht mehr viele in Europa, aber gerade deshalb ist ihre Festlegung von Wichtigkeit. Die Möglichkeiten der Anpflanzung, die Grenzen der Wirtschaftlichkeit der Bodennutzung und damit die Grenzen der Siedelungen erklären sich wiederum so oft aus der ursprünglichen Vegetation. Damit sind aber auch politische Grenzen und die Zeit der Besiedelung beeinflusst. Es ist besonders Gradmann, der hier schöne Zusammenhänge aufdeckte.

Die Klärung solcher Zusammenhänge kann nicht allein durch die in Einheiten gehenden kartographischen Darstellungen erreicht werden, sondern sie braucht auch Karten, die die grossen Züge darstellen, wie sie eben in einer Gesamtkarte eines Kontinents zum Ausdruck kommen.

<sup>1</sup> *Actes du III<sup>me</sup> Congrès international de Botanique, Bruxelles, 1910, T. 1, S. 97.*

Für die Pflanzengeographie selbst ist eine solche Darstellung dringend notwendig geworden. Die Pollenanalyse, die so viel wichtiges Tatsachenmaterial in wenigen Jahren zu Tage gefördert hat, die Florengeschichte, die Lebensgeschichte einzelner Arten und Gattungen—sie alle und neben ihnen die andern Zweige der Pflanzengeographie nicht minder—brauchen zur Deutung ihrer Ergebnisse die grossen Züge, wie sie nur in einer Karte eines Kontinents dargestellt werden können.

Wie wichtig es ist, dass die einzelnen Karten zu einer Gesamtdarstellung zusammengezogen werden, woraus sich erst die Hauptlinien ergeben, zeigt sich bei den geologischen Karten. Schon 1880 haben die Geologen auf ihrem Kongress in Bologna die Herausgabe einer internationalen Karte Europas beschlossen. Wenn auch die Durchführung viele Jahrzehnte beanspruchte, die Lebensarbeit von vielen Hunderten von Geologen umfasst, nur um die Unterlagen zu beschaffen, so hat sie doch ihre Früchte getragen. Durch sie sind erst die heutigen geologischen Kenntnisse des Baues Europas hervorgetreten.

Zu den Grundlagen der Geographie gehört u.a. die Vegetationskunde. Wenn wir aber die geographischen Handbücher durchsehen,—noch mehr, wenn wir uns in die Vorlesungen der Geographen an Hochschulen, leider selbst an vielen Mittelschulen, versetzt denken,—dann sehen wir, dass die Vegetationskunde, so nahe sie der Anthropogeographie steht, fast immer stiefmütterlicher behandelt wird, als beispielsweise die Geologie, die doch der Anthropogeographie viel ferner steht. In diesem Zusammenhang sei daran erinnert, wie viele der heutigen Geographen aus der Geologie gekommen sind und wie klein die Zahl derjenigen ist, die von der Botanik zur Geographie übergingen. Gewiss schiebt sich gewissermassen zwischen Pflanzengeographie und Geographie die Landwirtschaftslehre ein, aber auch zwischen Geologie und Geographie braucht es Brücken.

Nicht Mangel an Interesse, Missachtung der Wichtigkeit der grossen Züge in der Vegetationsverteilung, sondern die grossen Schwierigkeiten ihrer Darstellung haben die Pflanzengeographen abgehalten, neuere übersichtliche kartographische Wiedergaben zu versuchen. An Karten in grossem Masstab ist ja kein Mangel, fast jedes Land versuchte sich in solchen Einzeldarstellungen, wenn auch die stark von der Bodenproduktion beeinflussten Gebiete vernachlässigt wurden.

Wir bedürfen heute einer Karte, die das von Drude begonnene Werk ausbaut, die erschienenen Einzelkarten zusammenfasst. Es muss ein Masstab gewählt werden, der schon bereits Einzelheiten bietet und doch noch übersichtlich bleibt. Nehmen wir einen der Masstäbe, der denen unserer Wandkarten Europas entspricht, also etwa 1 : 20,000,000 oder 1 : 30,000,000, so können wir natürlich schon ganz bedeutend mehr einzeichnen, als es Drude und seinen Nachfolgern gelang. Aber Europa, besonders Westeuropa, ist ein Land stärkster wirtschaftlicher Beeinflussung, und alle diese Masstäbe erlauben nur die Eintragung der natürlichen Pflanzengesellschaften. Da diese vernichtet

oder umgewandelt sind, kann also nur die wahrscheinlich natürliche Vegetation, das Klimaxstadium, dargestellt werden. Ginge der Pflanzengeograph in konsequenter Weise vor, so käme er dazu, sowohl den Boden von Cambridge, wie den von London als von Laubwäldern eingenommen wieder zu geben, obschon hier Städte, Dörfer, Äcker, Wiesen und einige Heiden vorhanden sind. Wahrlich, weder Cambridge noch London liegen in einem Urwalde, noch ist unser gastfreies England eine Urwaldlandschaft. Aber in solchen Masstäben musste Europa bis jetzt gezeichnet werden. Dabei war es noch ausserordentlich schwierig zu wissen, in was die ursprüngliche Vegetation überhaupt bestanden hat. Wohl gibt es viele Gesichtspunkte, nach denen man eine Rekonstruktion vornehmen kann, aber es ist doch eben ein ganz theoretisches Vorgehen. Dabei wissen wir gar nicht, ob gerade in Europa, besonders im vergletscherten Gebiete, wo doch frühzeitig der Mensch einwanderte und die Vegetation beeinflusste, wirklich dieser Zustand jemals vorhanden gewesen ist. Sie wollen mich nicht so verstehen, als ob ich auf die theoretischen Rekonstruktionen keinen Wert legte. Schon die Erdkarte, die das Geobotanische Institut Rübel dem Kongress als Grundlage unserer Diskussion übergab, ist ja auf dieser Basis aufgebaut. Doch mir scheint, es wäre von grösstem Interesse, einen Schritt weiter zu gehen und eine Karte zu versuchen, die nicht nur die vermutlichen Klimaxstadien zeigt, sondern auch die heutigen Tatsachen der Vegetation mit ihren wirtschaftlich bedingten Änderungen der Pflanzenwelt.

Wenn wir eine pflanzengeographische Karte herstellen wollen, die nun schon die wünschenswerten Einzelheiten umfassen kann, so müssen wir zweifelsohne einen Masstab wählen, der die Eintragung von Einzelheiten erlaubt. Die internationale geologische Karte Europas hat den Masstab 1 : 1,500,000 und auf ihr können Gebiete eingezeichnet werden mit 1 mm. im Durchmesser; wenn es sich um streifenförmige Darstellung handelt, kann auch darunter gegangen werden. Sollte ein Vegetationsareal dargestellt werden, so müsste es in der Natur allermindestens die Grösse von 1,5 km. also etwa von einer engl. Meile, Durchmesser haben. Noch kleinere Gebiete liessen sich nur darstellen, wenn sie zusammenhängend, streifenförmig wären. Dazu wird vorausgesetzt, dass die Gebiete flächentreu dargestellt werden müssen. Dies ist allerdings nur bedingungsweise nötig, weder Flüsse, noch Strassen, noch alles was Signatur heisst, können ja in wahrer Grösse gehalten werden. Also wird man sich auch bei den kleinsten Flächen nicht zu streng an die wahre Grösse zu halten haben.

Die grossen Schwierigkeiten liegen nicht hierin, sondern sie ergeben sich bei Darstellung der Gebirge, z. B. in den Alpen. Schon die allmählichen Übergänge von Kultur zu Natur, die halbkultivierten Wiesen, die aus Wäldern entstandenen Weiden erhöhen die Schwierigkeiten. Und sie werden sehr erheblich, wenn die Talbreite nur auf wenige km. zusammengeht. Was kann in einem Alpental alles dicht beieinander vereinigt sein: unten

Weinberge und steppenartige Wiesen, Föhrenwälder, weiter oben Fichtenwälder, Lärchen- und Arvenwälder, nebst den Weiden der alpinen Stufe. Ein Masstab der auf ebenen Gebieten genügt, versagt im Gebirge, und doch muss man sich für *einen* Masstab entscheiden.

Damit haben wir schon begonnen, über Einzelheiten zu sprechen, und hier ist eine der ersten Fragen: Was für Anforderungen müssen denn überhaupt an die Unterlage gestellt werden?

Da ist in erster Linie zu sagen, dass schöne, gut ausgearbeitete Karten mit ihrer Plastik und ihren Farben nicht dienen können. Eine gute physische Karte passt uns nicht, denn auf die Farben, mit denen Ebene und Gebirge dargestellt werden, beispielsweise auf das in Grün gehaltene Tiefland und die rotbraunen Höhen, können keine neuen Farben aufgesetzt und keine weiteren Einzeichnungen gemacht werden. Auch die Schraffen und Schummerung einer Karte stören immer.

Andererseits bedarf natürlich der Pflanzengeograph einer Unterlage, die das Vorkommen von Pflanzen-Vereinen verständlich macht. Dazu gehören in erster Linie die Flüsse, die die Täler andeuten und die dazwischen liegenden Höhen wenigstens vermuten lassen. Die Flüsse dienen auch zur Orientierung. Je beschränkter im übrigen die Unterlage ist, desto besser, ausgenommen vielleicht einige wichtige Städte, Eisenbahnen usw., die ebenfalls zu einer raschen und sichern Orientierung beitragen. Wir brauchen also eine fast stumme Karte, nur mit Meeren, Seen, Flüssen und Bächen, die dagegen recht genau einzuzichnen sind. Ganz selbstverständlich sollen die Längen- und Breitengrade eingetragen sein. Eine Karte, in der noch Höhenkurven eingezeichnet sind, wäre von grossem Wert.

Was für eine Karte Europas gibt es nun überhaupt für unsern Zweck? Vor dieser gleichen Frage standen vor einem halben Jahrhundert die Geologen bei ihrem Kongress in Bologna. Es zeigte sich, dass es überhaupt keine brauchbare Unterlage gab. Jedes Land sucht eben für seine speziellen Bedürfnisse eine eigene Kartenprojektion. Die meisten europäischen Länder finden diese in einer Kegelprojektion, wobei dann ein oder auch zwei Breitengrade längentreu dargestellt sind. Um die Vergrösserung der Distanzen auf den Karten zu verringern, werden meistens kleine Korrekturen angebracht, sodass eigentlich keine echte Kegelprojektion mehr vorliegt. Daran, dass die Landkarten auch nur zweier benachbarter Länder zusammengestellt werden könnten, ist gar nicht zu denken. Geographische Europakarten als Wandkarten haben wir genügend. Da diese aber alle nur in Masstäben von 1 : 20,000,000 und noch kleineren gezeichnet sind, so kommen sie, wie schon gesagt, nicht in Frage. Die Geologen wählten für ihre Karte einen Masstab von 1 : 1,500,000. Nur dieser Masstab ermöglicht eine Karte, die als Handkarte und zugleich, wenigstens in Teilstücken, als Wandkarte benutzt werden kann. Die geologische Karte Europas umfasst 48 Blätter und wurde in 30 Jahren fertig gestellt. Für uns ist es eine sehr bemerkenswerte Tatsache: Hier

liegt eine ungeheure, selbstlose Vorarbeit vor, eine Karte deren Grundlage nur Meeresküsten, Seen, Flüsse und Bäche umfassend, ganz Europa einschliesst, und die zugleich erprobt ist.

Bevor wir uns aber zu einem Antrage entschliessen, müssen wir die Frage stellen, ob nicht seither eine neue Karte hergestellt worden ist. Das Bedürfnis nach solchen Karten war natürlich da, und da die Geologen auf die Darstellung von jedem Relief verzichten mussten, so genügte die blosser Unterlage den Geographen nicht. Schon auf ihrem Kongress von 1891 forderten diese eine Karte der ganzen Erde im Masstabe 1 : 1,000,000. Lange wollte die Angelegenheit nicht in Fluss kommen, bis England 1909 die Initiative ergriff und eine Weltkartenkonferenz einberief, die die Richtlinien festlegte. 1913 tagte die Konferenz in Paris. Daran nahmen 34 Staaten teil. Die 3. Konferenz tagte 1928 in Cambridge. Es waren 17 Staaten vertreten. Der jetzige Stand für Europa ist folgender: Der Europäische Block sollte 102 Blätter umfassen, davon sind nur 18 den Vorschriften entsprechend gedruckt, 25 haben abweichenden, 41 provisorischen Charakter. Afrika hat 3, Asien 15 und Australien 4 Karten. Daneben gibt es noch unfertige Karten oder solche mit Abweichungen von der Vorschrift. Die Karte zeigt Relief, und zwar mit Höhenkurven in braunen Tönen. Die Flüsse sind in Blau dargestellt, was mit farbigem Überdruck Mischöne ergibt. Für unseren Zweck sind dies nicht sehr günstige Verhältnisse, aber ein Umdruck in Schwarz, das Weglassen der braunen Höhenstufen, jedoch unter Beibehaltung der Höhenkurven, ist nicht mit grossen Kosten verbunden. Damit wäre für uns eine zweite Grundlage geschaffen. Wohl aber ist zu erwägen, dass die während des Krieges herausgegebenen Karten unbrauchbar sind, und in Deutschland und Österreich beispielsweise gibt es nur zwei Blätter: 1. Wien mit Prag und Breslau und 2. Ostpreussen. Wir sehen an diesem Beispiel, dass wir hier noch in den Anfängen stecken. Da aber auch vom Asiatischen- und Australischen Block fertige Karten vorliegen, von den andern Kontinenten ebenfalls mehrere, wenn auch mit Abweichungen von den Vorschriften, so ist die Sache doch sehr erwägenswert.

Fragen wir deshalb, was könnte der Masstab 1 : 1,000,000 mehr bieten als derjenige von 1 : 1,500,000. Am ehesten beantworten wir die Frage, wenn wir recht schwierige Gebiete ins Auge fassen. Da denken wir vorerst wieder an die Alpen, sind ihre Täler doch so tief eingeschnitten, dass sich hier Extreme berühren. In der Tat gelingt es, von der schematischen Darstellung von Waldstufe und alpiner Stufe abzuweichen und oft die tatsächlichen Vegetationsverhältnisse darzustellen, ohne gar zu grob schematisieren zu müssen. Zwei Muster sind zu Ihrer Orientierung ausgearbeitet worden: eines im Masstabe 1 : 1,500,000, das andere im Masstabe 1 : 1,000,000, beide umfassen das Gebiet vom Gotthard bis gegen Strassburg. Zweifelsohne kann die Karte 1 : 1,000,000 bedeutend mehr leisten. Zu dem kommt, dass unsere russischen Pflanzengeographen unter Leitung von Kusnezow vor allem ganz Hervorragendes fast mit dem gleichen Masstab gearbeitet haben. Die Darstellung



der grossen Züge war immer ein Vorzug der russischen Geographen, wenn ich nur an die Bodenuntersuchungen erinnern darf. Vergleiche der Europakarten mit denen der Russen im gleichen Masstabe wären von grossem Werte. Ein Zusammenfügen der Karten ist allerdings gar nicht denkbar, denn erstens ist der Masstab der russischen Karten nicht genau 1 : 1,000,000, sondern 1 : 1,050,000, zweitens ist das Gradnetz ein anderes. Aber die übrigen Karten sind im Masstabe 1 : 1,000,000 herausgegeben, sodass hier leicht Vergleiche gezogen werden könnten.

Ein grosser Nachteil ist, dass die Karte 1 : 1,000,000 als Wandkarte nicht mehr verwendet werden kann. Schon die geologische Karte von Europa stellt als Wandkarte sehr grosse Anforderungen an Raum und ist schon sehr unhandlich. Eine Karte 1 : 1,000,000 ist sicher keine Wandkarte mehr, nur noch eine Handkarte. So komme ich dazu zu empfehlen, mit weniger zufrieden zu sein und vorerst eine Karte 1 : 1,500,000 ins Auge zu fassen. Ihre Unterlage ist für ganz Europa durchgeführt, und die Ausführung könnte sofort an die Hand genommen werden. Es wäre verlockend eine Karte 1 : 1,000,000 zu besitzen, doch die Verwirklichung scheint mir noch in gar weiter Ferne zu liegen. Doch wenn ich zu einer Karte 1 : 1,500,000 rate, so ist dies eine ganz subjektive Ansicht, die andere gegenteilige Meinungen wohl versteht.

Andere Karten von Europa stehen nicht zur Verfügung.

Wenn wir heute eine pflanzengeographische Karte herstellen wollen, so sind wir merkwürdigerweise eigentlich fast frei von jeder Konvention. Wohl sprach schon 1910 Schröter davon, dass eine gewisse gemeinsame stille Übereinkunft bestehe: Die Steppen und Wüsten seien meistens in gelben, die Nadelwälder in grünen, die Laubwälder in violetten, die Gewässer und Sümpfe in blauen Tönen dargestellt. Eine Nachprüfung der in den letzten Jahren erschienenen pflanzengeographischen Karten zeigt, dass eine solche Konvention tatsächlich nur recht wenig beobachtet wird, ja, dass sogar der gleiche Autor die Farbgebung oft wechselt. Noch viel schlimmer steht es ja mit den pflanzengeographischen Zeichen. Doch bleiben wir vorerst bei den Farben. Die Ungleichheit der Farben macht das Kartenlesen mühsam. Jede Karte braucht zu ihrem Verständnis gewissermassen ein eigenes Studium und ein Vergleich ist sehr beschwerlich, für den nur etwas Fernerstehenden ausgeschlossen. Dem Geographen machen wir es wahrlich nicht leicht, sich unserer Karten zu bedienen. Mit Recht betont Scharfetter<sup>1</sup> (S. 80), dass Vergleiche aus den verschiedenen Florengebieten erst angestellt werden können, wenn einmal Arbeiten in möglichst gleichartiger Farbengebung vorliegen. Die Frage ist auf alle Fälle eine dringende und sie sollte vor, oder wenigstens gerade mit der Herausgabe der Europakarte geklärt werden. Unser wildes Chaos währt nun reichlich lange. Schon vor 50 Jahren sind die Geologen einig geworden, die geologischen Karten sind ohne Weiteres mühelos lesbar.

<sup>1</sup> SCHARFETTER, R. "Die kartographische Darstellung der Pflanzengesellschaften." Abderhalden, *Handbuch der biologischen Arbeitsmethoden*, Abt. 11, Teil 4.



Wird eine internationale Farbengebung aufgestellt, so muss auf alle Pflanzengesellschaften der Erde Rücksicht genommen werden. Wir europäischen Pflanzengeographen müssen den aussereuropäischen Pflanzenvereinen die nötigen Farben reservieren. Um die Verhältnisse in diesem Sinne abzuklären, möchte ich auf die Weltkarte hinweisen, die Sie bereits in einer kleinen Ausgabe erhalten haben. Sie ist entstanden durch die Umarbeitung einer alten Skizze von 1917 hauptsächlich durch das Personal des Rübel'schen Forschungsinstitutes. Auch die übrigen Farbenskizzen und die Zeichenvorschläge stammen von dort. Doch was Sie hier sehen, ist nur ein Teil der gemachten Vorarbeiten. Eine ganze Reihe von Beratungen und Besprechungen mussten stattfinden, um zu positiven Anträgen zu kommen. Ich möchte nicht unterlassen, Herrn Prof. Dr. Rübel meinen herzlichen Dank für diese weitherzige Unterstützung, die er dieser Sache angedeihen liess, auszusprechen.

Bei der Weltkarte gingen wir von folgenden Grundsätzen aus:

1. Wir wollten an das bereits Angewandte uns anlehnen. Es war für uns naheliegend, in erster Linie die Vorschläge der pflanzengeographischen Kommission der schweizerischen naturforschenden Gesellschaft in Betracht zu ziehen. Sie sind besonders vom früheren Präsidenten Prof. Rübel bearbeitet worden. Es zeigte sich, dass wir den Farbkreis zu sehr in Anspruch nahmen und beispielsweise grüne Töne für Wälder und zugleich für Wiesen gebrauchten. Wenn wir die Vielgestaltigkeit der Wälder berücksichtigen, so sehen wir, dass die Grüntöne dabei völlig aufgebraucht werden. Für die Wiesen bleibt kaum etwas übrig. Die von der pflanzengeographischen Kommission angewandten Farben mussten abgeändert werden und der Vorstand erklärt sich bereit, sich einer solchen Abänderung zu unterwerfen, wenn dadurch eine internationale Regelung in die Wege geleitet werden könnte. Von den bereits häufig angewandten Tönen lassen sich aber übernehmen: Blau für nasse Pflanzengesellschaften, Seen, Flüsse usw., Gelb für Wüsten, Steppen und ähnliches.
2. Bei der Farbengebung soll darauf Rücksicht genommen werden, dass in der Farbwirkung Gleichwertigkeit herrscht. Es sollen also nicht einzelne Töne herausknallen, herausstechen und die andern zurückdrängen. Die angestrebte Gleichwertigkeit hat aber ihre Grenzen. Gelb ist z.B. besonders in oranger Schattierung leuchtender als Stahlblau. Zudem: wir kommen mit den reinen Farben nicht aus, sondern müssen auch mit Schwarz und Weiss gemischte, also weniger leuchtende Farben, übernehmen.
3. Das Lesen einer Karte wird erleichtert, wenn der Ton der betreffenden Landschaft in ihr vorherrscht. Solche Töne helfen dem Gedächtnis und erleichtern besonders auch dem Fernerstehenden und dem Anfänger das Kartenlesen.
4. Ein ganz wichtiger Grundsatz scheint mir der zu sein, dass für verwandte Gesellschaften verwandte Töne verwendet werden. Diese Forderung ist gar nicht selbstverständlich, denn besonders der Détailforscher möchte gerne Besonderheiten hervorheben. Wenn beispielsweise in einem Nadelwald kleine

interessante Flecken von Laubwald vorkommen oder sich irgendwo ein Saum von Föhren mit steppenartigen Pflanzen zeigt, so ist es verlockend, diesen durch eine Kontrastfarbe hervorzuheben. Eine solche Farbenverwendung ist öfters angezeigt, sie wird übrigens auch von den Geologen ausgeübt, birgt aber in sich die Gefahr der zu häufigen und willkürlichen Anwendung.

Die Pflanzengesellschaften kennen selten scharfe Grenzen, meist ist es ein allmählicher Übergang. Karten mit grossen Masstäben können solche Übergänge wohl aufnehmen und der Forscher, der Einzelheiten angeben kann, wird nicht—und soll auch nicht—darauf verzichten wollen. Aber in einer Karte mit kleinem Masstab müssen diese vielen und oft nur subjektiv erfassbaren Übergänge wegfallen. Wählt man als Farben für verwandte, einander nahestehende Gesellschaften ebenfalls verwandte Töne, so wird die Schroffheit, die in der Verallgemeinerung liegt, gemildert. Ich glaube, auf der vorliegenden Karte ist der Übergang von trockenen Gesellschaften, von Wüsten und Hartwiesen zu den regengrünen Wäldern und schliesslich zu den immergrünen recht gut gelungen. Viel weniger befriedigend ist der Übergang gegen die Tundra. Die Taïga löst sich gegen die polare Baumgrenze langsam auf. Vorerst auf ungünstigen Böden, auf windexponiertem Gelände erscheinen Tundraflecken, bis sich diese verbinden und den Wald in einzelne Inseln auflösen. Wenn wir verwandte Pflanzengesellschaften mit verwandten Tönen bezeichnen wollen, so müsste auch hier ein Übergang sein und diese harte, auch an sich hässliche Grenze sollte sich in eine weiche Übergangszone auflösen. Das ist nun leider hier nicht möglich. Der Fehler liegt in der Natur der Farben. Die Farben lassen sich als Band oder als Kreis darstellen, sie sind eindimensional. Die Pflanzengesellschaften aber sind so mannigfaltig, dass nur ein vieldimensionales Farbensystem genügen würde, um eine ideale Darstellung zu geben. Ein Übergang vom Trockenen ins Feuchte und Nasse lässt sich darstellen, nicht aber zugleich ein Übergang ins Kalte. Das Ideal, verwandte Töne für verwandte Pflanzengesellschaften, ist nur einmal verwendbar und ist hier für die Übergänge vom Trockenen ins Nasse angewandt worden.

5. Ich glaube, wir sind uns alle klar, dass nur durch Farben die Pflanzengesellschaften auf grossen Karten übersichtlich dargestellt werden können und deshalb müssen diese normiert sein. Wir haben uns also nun zu fragen: Welche für uns brauchbare Farbenkodes kommen in Frage? Dann müssen wir weiter gehen und sehen, ob sie im Handel sind, ob die betreffenden Farben auch gedruckt werden können und dabei der Druck nicht zu grosse Schwierigkeiten bereitet. Nun sind wir Pflanzengeographen nicht die einzigen, die Farbenormen brauchen, auch die Maler und besonders die Techniker haben fast die gleichen Wünsche. Es wird gut sein, wenn wir uns umsehen, was dort geschieht. Dass unsere Systematiker so wenig mit Farbenormen arbeiten und in ihren Beschreibungen sich mit den so wenig genauen Bezeichnungen wie Blüte blau oder gelb oder rot begnügen, ist eine Sache für sich.

Ein älterer, weitgehender Farbenkodex ist derjenige von Valette und

Klincksieck, Paris 1908. Neuere Zusammenstellungen verdanken wir Ostwald, der mehrere Farbenlehren herausgegeben hat und daher systematisch vorgeht. Ostwald stellt seine Farben kreisförmig zusammen und rechnet mit vier Urfarben: Gelb, Rot, Blau und Grün. Zwischen diese bringt Ostwald noch je 5 gut unterscheidbare Töne hinein, sodass er zu 24 Vollfarben kommt. Darunter versteht er reine Farben, also solche, die weder Weiss- noch Schwarzgehalt aufweisen. Durch Zusetzen von Weiss oder Schwarz, oder schliesslich Weiss und Schwarz zugleich, wird der Ton verändert. Von jedem Ton können solche Abänderungen hergestellt werden. Dies zeigt sich am besten durch ein farbengleiches Dreieck, wo der Ton zweidimensional abgeändert wird: durch Beimischung von Weiss, durch Zugabe von Schwarz und dazwischen durch eine Beimischung von beidem. Wir sehen, wie im entstandenen farbengleichen Dreieck viele neue Töne herausgekommen sind. Der Pflanzengeograph kann von ihnen nicht alle gebrauchen. Zu starke Schwarzmischung macht zu dunkel, zu starke Weissmischung zu hell. Aber aus diesen Tönen können wir doch mindestens 8 herauslesen, sodass  $8 \times 24$ , als 192 Töne zur Verfügung stehen.

Zweifellos berührt die Verwendung aller dieser Töne nicht angenehm. Nur wenn Töne mit gleichem Schwarz- und Weissgehalt untereinander im gleichen Abstand verwendet werden, sind sie unter sich harmonisch. Wir sind aber gezwungen, viele und unterscheidbare Farben herauszubekommen, und deshalb kann das Kartenbild nicht harmonisch bleiben. Wie wünschenswert wäre es, nicht nur eine sachlich klare Vegetationskarte zu erhalten, sondern auch eine solche mit harmonischen Tönen. Das ist nun leider nicht denkbar. Dass wir auch hierüber Studien gemacht haben, zeigen diese drei Karten, wobei nur klare Farben, also ohne Weiss- und Schwarzgehalt, verwendet wurden. Sie sehen, wie auf diese Weise der ganze Farbkreis schon verbraucht ist. Doch hier sind ja nur die klimatisch bedingten Pflanzengesellschaften dargestellt. Daneben sind noch die edaphischen und die Kulturformationen zu berücksichtigen. Für diese blieben keine Farben übrig. Doch in einer Beziehung, so scheint mir, sollte die Verwendung der Töne festgelegt werden: Für extreme Gesellschaften schlage ich vor, die Urfarben zu verwenden, nämlich:

		Valette und Klincksieck	Ostwald	Tanner
1. Trockenwüsten	gelb	206	1	18/1
2. Kältewüsten	rot	26	7	18/65
3. Tropische Regenwälder	grün	356	19	18/185
4. Plankton, Sümpfe	blau	426	13	18/137

1. *Trockenwüsten*. Gelb wurde für die Wüste sehr häufig verwendet, und da der Mangel an Grün für uns das Charakteristische der Wüste zu sein scheint, so haftet der gedächtnismässige Eindruck. Von diesem Gelb kann sehr leicht in allen Abstufungen das Grün erreicht werden.

2. *Kältewüsten*. Diese kommen in der Nähe der Pole, aber auch in grösserer Meereshöhe vor. Für Gebirge wurde schon vielfach Braunrot verwendet,

sodass dadurch dieser Ton verständlich ist. Bereits Drude hat diesen Ton für Kältewüsten verwendet.

3. *Regenwälder*. Die stärkste Pflanzenentwicklung mit Grün zu bezeichnen ist gegeben, trotzdem wir zugeben, dass bei dem grossen Wechsel der Pflanzengesellschaften die verschiedenen Abstufungen von Grün schwer durchzuführen sind.

Die zwischen diesen extremen Fällen liegenden Pflanzengesellschaften sollen Zwischentöne erhalten und zwar, soweit möglich, nach dem Grundsatz: ähnliche Pflanzengesellschaften—ähnliche Töne.

Ist auf diese Weise beispielsweise für einen Nadelwald ein Ton gewählt, so bliebe dieser für alle Nadelwälder bestehen, aber durch Beimischung von Schwarz und Weiss würden Abstufungen erreicht.

Auf diese Weise kommen wir zu den Farben der Weltkarte. Die verwendeten Farben beschränken sich auf wenige Töne, denn wir mussten Farben freilassen für Wiesen, Sümpfe, Plankton und Kulturen. Vom ästhetischen Gesichtspunkt aus ist gewiss nicht alles so, wie es wünschenswert wäre. Gewiss kann noch vieles geändert werden, doch, das scheint festzustehen, auf vollkommene Harmonie muss verzichtet werden. Der Fehler liegt nicht am Sehen oder Durchdenken, sondern darin, dass die Zahl der Farben, die das menschliche Auge sieht, eben beschränkt ist.

Die Pflanzengeographen sind, wie schon erwähnt, nicht die einzigen, die heute Farbnormen festlegen wollen, auch die Techniker stehen vor der gleichen Aufgabe. Doch schon längst haben sich jene in kleinerem Kreise geeinigt, wie auf ihren Plänen die Farben zu verwenden sind, durch welche Töne z.B. Altes und Neues, verschiedene Metalle, Art des Mauerwerkes, Drehstrom und Wechselstrom und dergleichen darzustellen ist. Auch haben meistens die nationalen Technikerverbände ihre Farben festgelegt, und, was sehr wichtig ist, man kann diese Farben im Handel erhalten. Dies sind eminente Vorteile. Das Anlegen von Skizzen, Plänen, aber auch von Drucken wird gefördert, das Lesen erleichtert. Ostwald hat nun den sehr grossen Vorteil, dass seine Töne zugleich als Deck- und Wasserfarben ohne Weiteres zu billigem Preise käuflich sind. Auch seine Farbtafeln sind verbreitet und wohlfeil. Doch ist in diesem Farbensystem noch alles im Flusse. In Bern ist ein Weltfarbeninstitut gegründet worden und es ist zu erwarten, dass die Ingenieure durch den Internationalen Normungs-Ausschuss Isa in Zürich sich auf bestimmte Farbengebung einigen. Damit wäre auch uns gedient, da dadurch der Druck der Karten eminent erleichtert würde. Es ist dann auch denkbar, dass dies in jeder beliebigen Druckerei geschehen könnte.

6. Hand in Hand mit der Farbengebung sollten wir uns auch über die Zeichengebung einigen. Wenn auch viele Farben zur Verfügung stehen, so ist das Farbenlesen nicht Jedermanns Sache. Die Empfindlichkeit, verschiedene Farbtöne zu unterscheiden, ist verschieden, aber auch die Farbenwirkung hängt von der Umgebung ab. Wie die Geologen für kleine Flächen einen

Aufdruck von Buchstaben und Zeichen brauchen, so auch die Pflanzengeographen. Eine Zusammenstellung der in den letzten zehn Jahren in Europa verwendeten Zeichen zeigt eine Willkür sondergleichen; ja der gleiche Autor wechselt seine eigenen Zeichen ganz launisch. Die von der schweizerischen pflanzengeographischen Kommission vorgeschlagenen Zeichen wurden recht konsequent in der Schweiz, dann aber fast nur von Issler im Elsass und von Salisbury in England verwendet. Das ist für mich fast eine Enttäuschung. Wer eine Karte mit neuen, noch nicht bekannten Zeichen herausgibt, wer seine Zeichen launisch ändert, ahnt wohl nicht, wie er selbst das Lesen seiner Karte erschwert. Er muss nicht erstaunt sein, wenn so wenig auf seine grosse Arbeit Bezug genommen wird und die verwandten Disziplinen fast achtlos daran vorbeigehen.

Die zu wählenden Zeichen müssen so einfach sein, dass sie immer, sowohl bei der Feldarbeit, wie auch im Drucke verwendet werden können. Gedruckte Zeichen müssen bei einer Höhe von 1 mm. noch kenntlich bleiben. Aber nicht nur als Einzelzeichen, sondern auch als Flächenzeichen sollten sie verwendbar sein; nicht für die geplante Europakarte, aber für in Schwarz zu druckende Karten. Denn sehr oft sind eben auch die Gelder nicht da, um vielfarbige Karten zu drucken. Auch kleine Skizzen, die in den Buchtext hineingehören, sollten sich klar und billig darstellen lassen.

Damit bin ich zum Schlusse gekommen. Unsere Schwesterwissenschaft, die Geologie, hat sich schon längst zu einheitlicher Farb- und Zeichengebung aufgerafft. Die geologischen Karten und Arbeiten sind sehr verbreitet, und die Rolle, die sie in andern Wissenschaften, z.B. in der Geographie spielen, ist Ihnen genügend bekannt. Wie wenig verbreitet sind unsere Karten und es ist fraglich, ob wir nicht selbst daran etwas Schuld tragen. Die vorhandenen Karten sind meist Einzelkarten. Es fehlt ihnen die Eingliederung in das Grosse, das Ganze, in Übersichtskarten. Auch sind sie nicht leicht und rasch lesbar, da weder Farben- noch Zeichengebung einheitlich ist.

Ich wende mich an Sie alle. An der Spitze dessen, was wir bedürfen, steht eine Vegetationskarte Europas. Was die Geologen in grösserem Masstabe vor einem halben Jahrhundert begannen und in so wunderbarer Weise auch durchgeführt haben, muss auf dem Boden der Botanik ebenfalls möglich sein. Ich bitte Sie, helfen Sie mit, jeder an seinem Ort.



# THE ECOLOGY OF THE AYRELAND OF BRIDE, ISLE OF MAN

BY E. J. MOORE.

*(With Plates X to XIII, and two Figures and 1 Map in the Text.)*

## INTRODUCTION.

THIS paper is concerned with the ecology of a post-Pleistocene raised beach, together with that of the present beach, situate at the extreme north of the Isle of Man.

The natural vegetation forms a strip of heathland fringed by a narrow zone of maritime vegetation occupying the blown sand, whilst the remainder of the former beach is now occupied, on the landward side, by an area of poor agricultural land reclaimed from a former more extensive heath during the last century.

The area studied exhibits several features of interest: (*a*) it bears a heath which must be regarded as primitive in that it is occupying a shingly soil not previously occupied by a former vegetation; (*b*) the age of the beach, in geological time, is known, as is the geology of the underlying strata; (*c*) the north of the Isle of Man is covered by a mantle of glacial drift deposited during an Ice Age when the whole of the island was covered by an ice sheet, so that the plants forming the present vegetation of the island must have occupied the land since the melting of this ice cap; (*d*) the reclamation of parts of the heath to form farm land has been relatively recent and the methods adopted are known.

## GENERAL PHYSIOGRAPHIC AND GEOLOGICAL CHARACTERS OF THE ISLE OF MAN.

The Isle of Man is one of the smaller British Isles situated in the Irish Sea, and roughly equidistant from England, Scotland and Ireland, from which it is now separated by deep channels, though formerly land connections most probably existed during the upheavals in the Pleistocene period (6, 7).

The geology of the island, which has been worked out fully by Lamplugh (8, 9) who embodies some of the work of Cumming (3) and Boyd Dawkins (1, 2), indicates that not only has the region been subjected to considerable earth movements, both upheavals and subsidences, but that the whole island was completely buried under a glacial sheet of the most recent Ice Age, this sheet attaining a maximum elevation of not less than 2000 to 3000 feet above the present sea level. The approximate movement of the ice sheet was from N.N.W. to S.S.E., as indicated by the presence of erratic boulders carried from Ailsa Craig in the Firth of Clyde.



Thus the north of the Isle of Man at the present time comes to be covered by a thick layer of glacial drift, deposited on a floor of Palaeozoic rocks, forming a plain north of a line drawn roughly from Ramsey to Peel, which indicates a former shore line. This layer, reaching a maximum thickness of about 450 feet at Bride, is evidently glacial detritus derived from melting ice in the form of both glaciers and bergs (1), and is composed of material foreign to the rest of the island.

#### THE AYRE.

##### Physiographic and Geological characters.

The Ayre is a barren strip of shingle at the northern extremity of the drift plain previously mentioned, rising from 10 to 25 feet above high-water mark, and covered in places by low dunes of shifting sand. To the east its width is  $1\frac{1}{2}$  miles, but as it passes westward it gradually narrows to a strip 50 yards or so in width, appearing like a storm beach, the entire length being about  $4\frac{1}{2}$  miles.

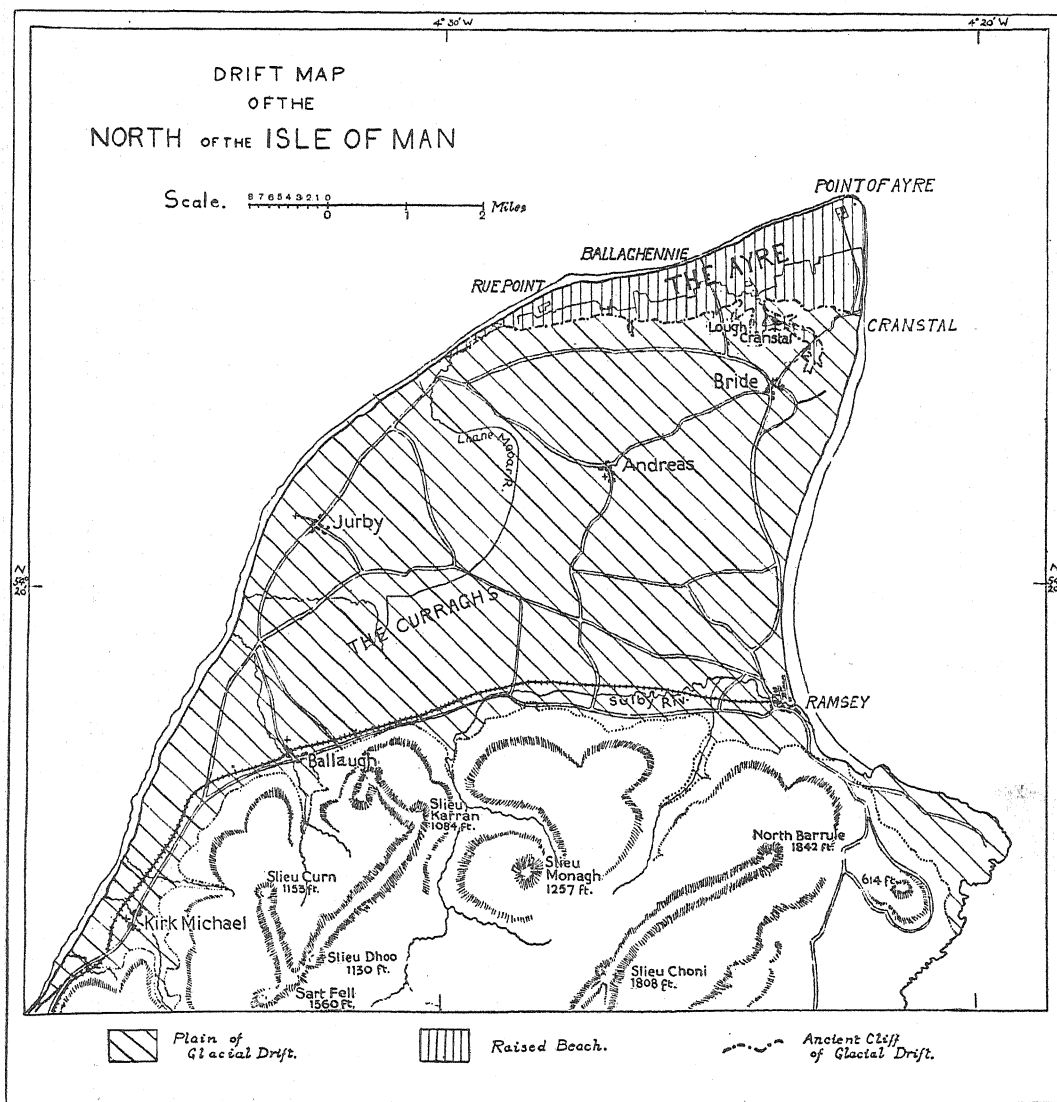
This shingle zone is undoubtedly a raised beach and represents the only post-Glacial marine deposit, above the present sea-level, recognisable in the island. Its landward limit is sharply defined by ancient cliffs carved out of the original drift deposit, the height of these cliffs being about 90 feet above high-water mark at the Point of Ayre. The beach must have been slowly rising during the Neolithic period, though the completion of the elevation occurred later, for the surface of the inner parts of the region bears numerous chipped flints of Neolithic workmanship, whereas these are absent from the more seaward margin. The north end of the island was being gradually tilted upwards and slightly to the west, as the beach at the Point of Ayre has a height of about 25 feet, whereas to the west it is only about 15 feet.

There is a local belief (and this must be of long standing, as it is given as a fact by Cumming (3), who, however, never visited the shore), that land is still "gaining on the sea" in this region, evidently based on the fresh aspect of the bare shingle ridges, but the records, both of the Ordnance Survey of 1869, and the plans of the Commissioners of the Northern Lights, of 1815, show that there has been no recent addition of land, but rather a slight erosion of the coast, as is to be expected on a shore exposed to the open sea.

Lithologically the raised beach consists of pebbles of varying size and constitution, along with some blown sand and occasional broken shells. The pebbles are up to 9 inches in diameter and consist of grits, quartzites, vein quartz, red and purple sandstones, sandy slate, conglomerates, flint, diabase, basalt, felsite, mica trap, mica schist, gneiss, granites and carboniferous limestone; so that such a "soil" is both very porous and poor in lime, and in most instances weathers slowly. Those shells found are of present forms of the neighbouring sea, including oyster, mussel and whelk.

The blown sand, occurring on the shingle of the Ayreland, is not large in

quantity, owing, partly, to the absence of estuarine silt, and to the occurrence of deep channels close inshore, which tend to wash detritus seaward, and partly to the absence from this region of suitable rock which would weather to form sand.



Sand forms a fairly even covering on the inner part of the raised beach, and it is a strip of this which has been enclosed for agricultural purposes. The inland zone of blown sand is of long standing, as is evidenced by the occurrence of Neolithic flints on the surface, and because it was used in the same period for the raising of burial tumuli, of which there are several in the

area. This inland region probably represents the maritime fringe of the time when the sea level was higher.

There is also a narrow strip of blown sand along the shore, but this is small in amount, and though forming low dunes in some places, is generally in the mobile state, gradually moving from west to east along the shore whence it apparently disappears into the sea. There is no deep zone of dunes as is found in those coastal regions with more abundant blown sand.

The present beach is a fairly steep narrow zone of shingle and pebbles with a small ridge of sand exposed at the lowest tides. The pebbles are similar in size and composition to those of the raised beach.

There is an absence of springs and streams from the region, though at one point there is a ditch leading water on to the Ayre from a low-lying inland marsh, but the water from this gradually percolates through the subsoil and disappears at a point about 400 yards from the sea. Several wells have been sunk through the shingle and the average depth is 25 to 30 feet, water being replenished by the percolation of surface rainfall, supplemented by drainage from the Bride hills.

The depth and nature of both the shingle of the raised beach and of the glacial drift beneath have been fully investigated by Prof. Boyd Dawkins (1, 2) who superintended the series of borings made along the north coast of the island during a survey for coal. These borings indicate the depth of the raised beach, consisting of sand, shingle and pebbles, to vary from 15 feet at Ballaghennie to 25 feet at the Point of Ayre, i.e. the soil and subsoil are practically identical. There was no indication in the borings of any peaty material or other evidence of a previous land surface with vegetation, though it is of interest to note that post-Pleistocene peat deposits in the drift at Kirk Michael, some few miles inland, have yielded the Arctic species *Salix herbacea* and *Carex alpina*.

#### Rainfall and Wind.

Since 1825 the records of rainfall and wind, at the Point of Ayre, have been kept by the keepers of the lighthouse, and it is to them and to the Commissioners of Northern Lights, Edinburgh, that the writer is indebted for the rainfall figures for the years 1917-27, and for a wind summary over the same period.

The mean annual rainfall for the area is relatively low, being lowest during the spring and summer months, when parts of the vegetation become scorched, and highest during the winter, though the actual difference is not very great. The mean annual rainfall for the period 1917-27 was 27.44 inches, being highest in 1921, when 31.36 inches were recorded.

The wind records show a prevalence of winds from the western half of the compass (in 1917 the wind blew from a westerly direction on 177 days, and from an easterly direction on 116 days; in 1927 the figures were 188 and 107 respectively), and this has an effect on the disposition of the blown sand, which tends to be moved eastwards.

The strongest winds are those from the N.W. and N.E., which blow against the seaward fringes of the raised beach and frequently serve to throw up the higher tides on to the lower parts.

### Biotic Factors.

The Ayreland, being a sandy area away from any great human activity, has been colonised by rabbits, which here reach a density greater than elsewhere in the island.

The rabbits graze on the grasses and the more juicy shoots of the xerophytes, keeping the vegetation closely cropped in the case of some communities, and causing the formation of hummocks in others. Another effect, where rabbits occur in sandy regions, is the formation of "blow-outs" by the scraping away of the consolidating surface vegetation during burrowing, ultimately resulting in the creation of areas of bare sand which become re-colonised in a definite succession.

The Ayreland is also used as a pasturage for small flocks of sheep and an occasional goat, and their grazing has the same general effect on the grasses as the rabbits', in keeping a close-cropped turf.

Another factor tending to prevent a stabilising of the dune vegetation is the practice of "pulling bent" (*Ammophila*) for the purpose of thatching stacks and farm buildings. This occurs on a moderate scale at the end of the summer, when the grass on the mobile dune area is either uprooted, or cut with a scythe, so forming areas of comparatively open sand which is then subject to the effects of wind. This treatment of the plant stimulates it to spread outwards and so prevents the upward growth of a dune, and it is a fact that nowhere on the Ayre is there a very high dune.

### The Vegetation of the Ayre.

The vegetation of the Ayreland has not previously been studied in detail, but a brief description of the region is included in a summary account of the Manx dune flora by Wheldon and Hartley (12). Although this description includes an ecological classification of the vegetation, the limits suggested are very broad, such that the Ayreland is included in a "Marham with Heather Association" which the present writer considers to be an area of several distinct plant communities, the relations of some of which are rather uncertain.

The communities recognised in the present paper (some of which have developed as a result of biotic influence) may be classified as follows:

1. The shingle beach.
  - (a) A sand and pebble shore community.
2. The region of blown sand.
  - (a) Community of *Ammophila arenaria*.
  - (b) Community of the consolidated dune slope.
  - (b i) Secondary succession following rabbit activities.

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3. The vegetation of the raised beach.

A. Dry types.

- (a) Heath, dominated by *Calluna vulgaris* and *Erica cinerea*.
- (a i) Secondary succession following burning.
- (a ii) Secondary succession following rabbit activities—"hummock" heath.
- (b) Community of *Ammophila* on hummocks—relict (?).
- (c) "Creggans"—community of *Ulex europaeus*—invading the heath.
- (d) Community of *Pteridium aquilinum*—invading the heath.

B. Damp types.

- (e) Neutral grassland.
- (f) Ditch from Lough Cranstal.

4. Arable land.

1. THE SHINGLE BEACH.

(a) *Sand and pebble shore community.*

The present beach consists of a narrow strip of shingle and pebbles forming a relatively steep cliff around the Point of Ayre. The pebbles have been thrown up, by the two tides which meet at the north of the island, into terraces parallel to the shore line, and these are completely submerged during the higher spring tides, and during storms. During the lower tides the uncovered portion of the beach is but a thin strip formed of large pebbles and shingle.

The pebbles vary in size from a fraction of an inch to 9 inches in diameter, being flattened by wave action; a small amount of sand occurs between the pebbles, some of it having subsided on to the shore from the fringe of blown sand above.

Occasional plants of the lichens *Lecanora* and *Lichina* occur on the larger pebbles, both between the high and low water marks and above the normal high-tide mark.

There is little tidal debris in the form of seaweed, owing to the absence from the vicinity of rocks which would bear a seaweed flora.

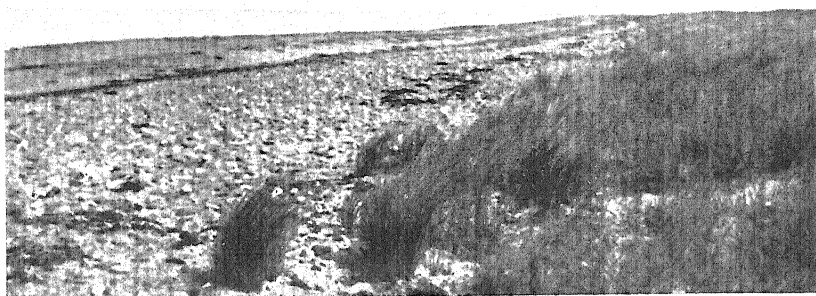
The beach flora is scanty, and poor in floristic composition, species occurring as solitary plants rooted in the shingle amongst the larger pebbles. Plants of *Cakile maritima* are found which owe their presence to the fact that the fruit had become wedged between large pebbles, germination having occurred in an apparently inhospitable situation. The species occurring in this region are halophytic and consist of the following:

<i>Cakile maritima</i> <sup>1</sup>	o.	<i>Atriplex patula</i>	o.
<i>Arenaria peploides</i>	o.	<i>Salsola Kali</i>	o.
<i>Matricaria inodora</i>	r.	<i>Atriplex hastata</i>	o.

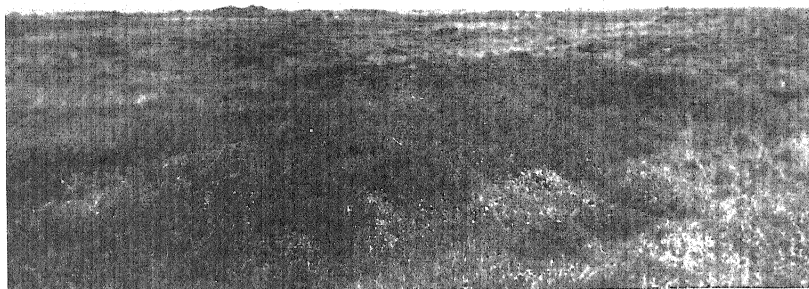
At those points on the shore where blown sand has accumulated, there

<sup>1</sup> The nomenclature of the *London Catalogue of British Plants*, 11th edition (1925), is followed.

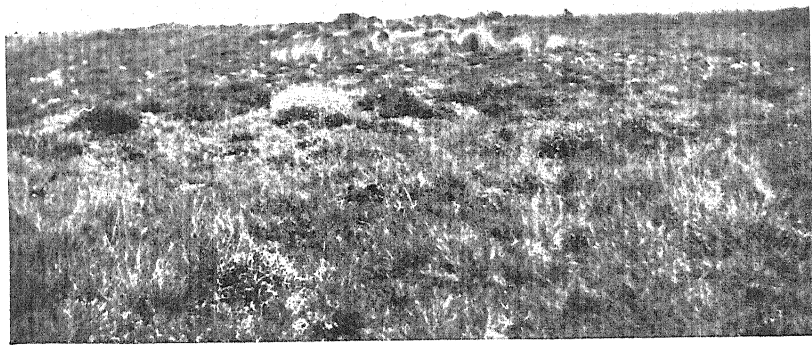




Phot. 1. View of the shore near Rue Point, looking N.E. A scanty strand vegetation occurs here, and the blown sand is accumulating to form a low bank, due to the growth of *Ammophila arenaria*. The higher spring tides reach the lower limits of this dune-bank, as is evidenced by the tidal debris.



Phot. 2. A general view of the heath of the raised beach, dominated by *Erica cinerea* and *Calluna vulgaris*. In the centre is an area dominated by *Ulex Gallii*. The characteristic grass is *Festuca ovina* which occasionally becomes temporarily dominant during the succession following rabbit attack.



Phot. 3. Another view of the heath of the raised beach, in a region abounding in rabbit "runs." Here a turf is formed by heath grasses, the usual dominants occurring in clumps here and there. Note the presence of persistent *Ammophila* on the heath.





may be a subsidence of sand on to the pebbly beach, and this is followed by an invasion by *Ammophila* from the blown sand community above.

In several instances, where the action of wind and tide has resulted in the formation of a relatively steep dune-face, the subsidence of land on to the beach is accompanied by the fall of pieces of *Ammophila* rhizome, which may ultimately serve to build up a less steep dune bank.

In all cases where *Ammophila* has invaded the shore community, the plants are subjected to submergence during the higher tides and seem to suffer no harm.

## 2. THE REGION OF BLOWN SAND.

At the present time, there is a striking absence from the Ayre of the usual dune succession met with on the coast at many points in the British Isles. This is due partly to the lack of abundant blown sand, and partly to the fact that the wind does not appear to remove the sand inshore so much as along the shore from west to east, where the zones of vegetation are stabilised and correspond, in a simplified form, with the typical succession on a sandy shore where the land is advancing.

### (a) *Community of Ammophila arenaria.*

From Rue Point to Ballaghennie a low lying region of sand approaches the pebbly beach, and this, though clear of the ordinary high tides, is partly submerged when the spring tides prevail, as is indicated by the tidal debris thrown up on to the sand.

The dominant plant is *Ammophila arenaria*, which occurs exclusively as the early colonist, spreading by its rhizomes and acting as a sand-binder, retaining the sand blown amongst its tufts. The sand gradually accumulates to eastward, forming a low barrier, hardly to be designated "dunes," some 12 yards deep and from 3 to 10 feet above the present shingle beach, being heaped up on the fringe of the raised beach. *Ammophila* occupies the whole of this blown sand zone, both the seaward and landward faces, but never forming a really dense covering, so that the sand is always more or less shifting.

The other species which occur here are present as occasional plants between the tufts of Marram Grass: they include the rare and local *Brassica monensis*.

The species noted in this zone are as follows:

<i>Ammophila arenaria</i>	Dom.	<i>Senecio jacobaea</i>	f.
<i>Brassica monensis</i>	r.	<i>Hypochaeris radicata</i>	o.
<i>Cakile maritima</i>	o.	<i>Leontodon taraxacoides</i>	o.
<i>Ononis repens</i>	f.	<i>Calystegia Soldanella</i>	o.
<i>Eryngium maritimum</i>	l.a.	<i>Atriplex</i> sp.	o.
<i>Matricaria inodora</i>	r.	<i>Festuca rubra</i> var. <i>arenaria</i>	f.

### (b) *Community of the consolidated dune slope.*

The lower part of the landward slope of the dune bank, owing to its comparatively greater shelter, becomes occupied by more abundant species which

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ultimately consolidate the sand to form a covering turf which gradually merges into the main heath of the raised beach. Those plants assisting in the consolidation are mainly *Carex arenaria*, *Festuca rubra*, *Thymus serpyllum*, and *Lotus corniculatus*, all of which have good methods of vegetative reproduction.

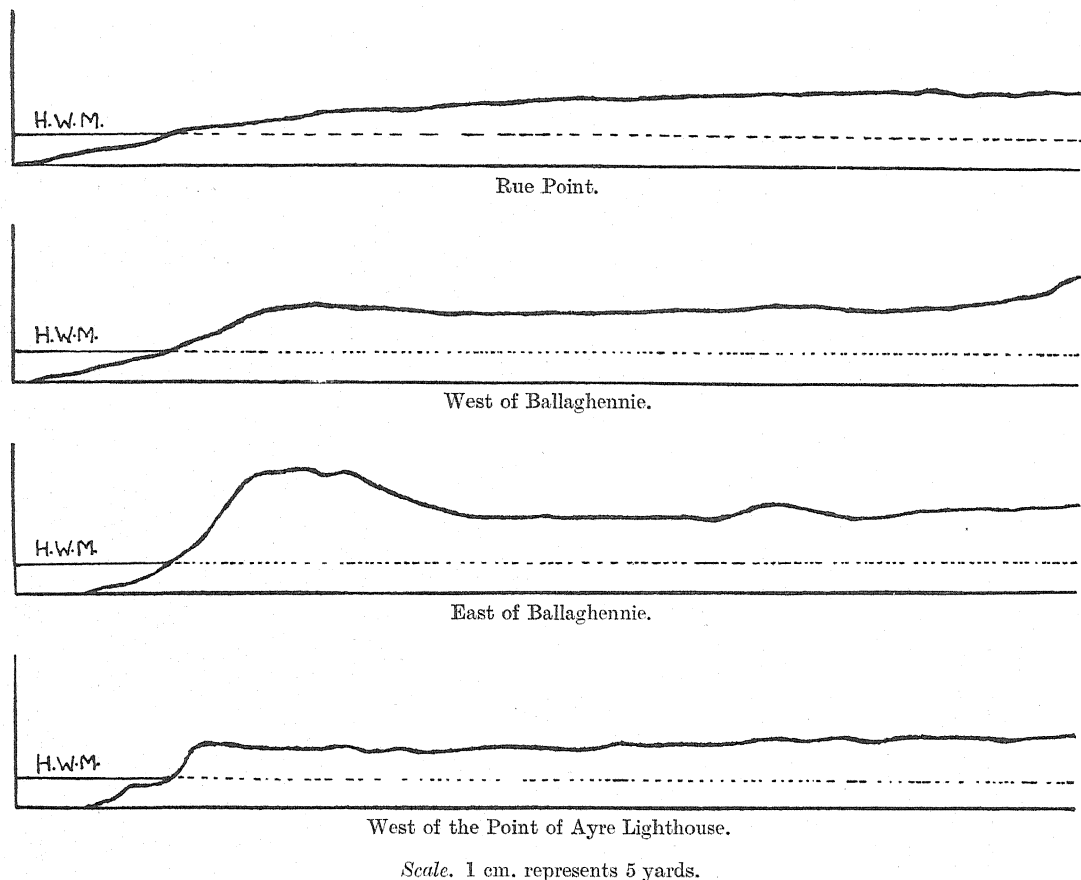


Fig. 1. Rough sections through the seaward margin of the raised beach, progressing from west to east. The series indicates the way in which blown sand accumulates to eastwards. This sand is ultimately blown across the heath and is not represented on the shore as the Point of Ayre is approached.

A similar consolidation of the blown sand is found along the shore as the Point of Ayre is approached. The relation between the consolidated slope and the heath of the raised beach is not clear, but as there is a certain similarity in the floristic composition of the two communities, it seems possible that the former passes into the latter as leaching and the accumulation of humus occurs.



(b i) *Secondary succession following rabbit activities.*

Rabbits abound in the region and use the dune slope both as a grazing centre and as a site for the construction of warrens. Their activities result in the subjection of those species used as food, and also in the clearance of certain areas, owing to the loosening of the surface sand. The burrowing and scraping of rabbits cause the appearance of "blow-outs," for, once the surface vegetation of the slope and some of the underlying sand are removed, the wind assists in the creation of small or large areas of bare sand. These areas are recolonised by the neighbouring species. The bordering grasses and herbs *Festuca*, *Galium*, *Thymus* and *Rosa* encroach on the margin by vegetative means, but the central bare region undergoes a succession which, from the study of several clearings, is shown to be fairly constant.

The usual stages in the succession consist of the following:

- (i) Lichen stage.
- (ii) Moss stage.
- (iii) *Sedum anglicum*—*Carex arenaria* stage.
- (iv) Normal sward community.

(i) The first colonists of the bare soil are lichens, particularly *Cladonia*, and occasionally *Parmelia* and *Peltigera*, and these become scorched up in the summer months to form a scanty humus.

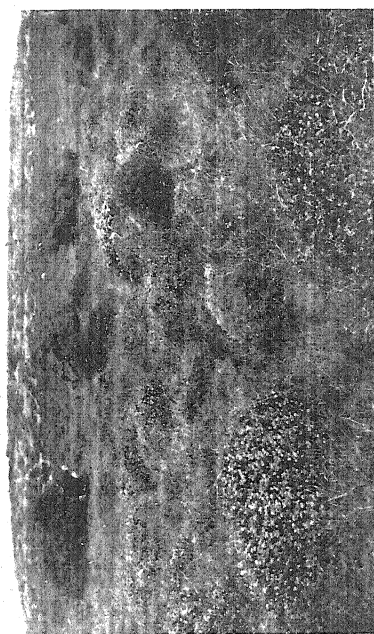
(ii) The lichens are either accompanied or followed by *Polytrichum* which forms dark patches in the clearing, and other mosses may also occur, such as *Tortula* and *Hypnum*.

The lichens and mosses serve to stabilise the soil surface and prepare the way for the subsequent colonists.

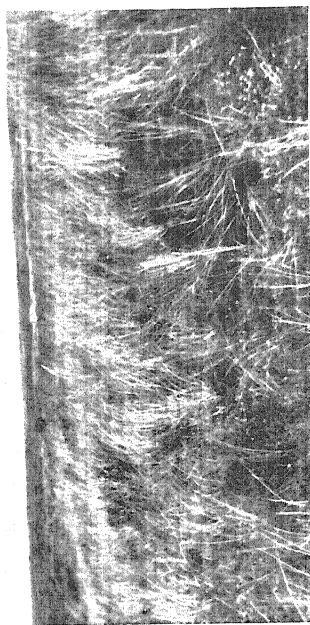
(iii) The stabilisation of the soil having proceeded, phanerogams begin to arrive in the clearing. Some spread from the margin, particularly *Carex arenaria*, which does so by means of its efficient rhizome, whereas others develop from seed. The first phanerogam to appear in the more open part of the clearing is *Sedum anglicum*, which spreads rapidly, both vegetatively and from seed, and it may be accompanied by seedlings of *Carex*. Both *Sedum* and *Carex* appear to be immune from rabbit attack, which may account for their early appearance.

(iv) By the time that the clearing has become stabilised again, other species, characteristic of the vicinity, have arrived, including *Festuca* spp., *Agrostis* sp., *Thymus serpyllum*, *Lotus corniculatus*, etc., which spread rapidly and complete the formation of a sward, which is then typical of the dune slope.

*Carex arenaria* may persist in patches, but usually it becomes more subdued, as other vegetation covers the clearing, and is represented by occasional tufts only.



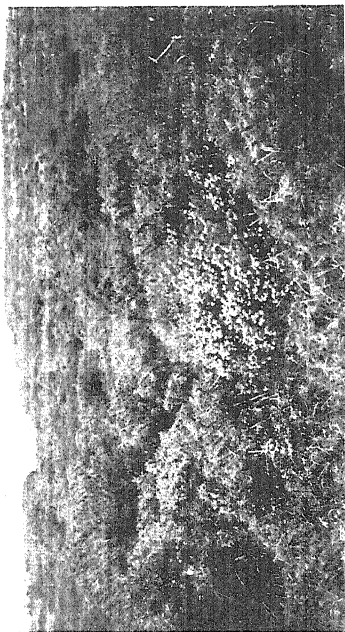
Phot. 5. Grass heath phase of the recolonisation of hummock heath. The main hummocks are composed of *Erica cinerea* (in flower) and *Calluna*, with, occasionally, a larger bush of *Ulex Gallii*. Heath grasses and *Carex arenaria* form the ground vegetation.



Phot. 7. A low sand-hill on the inland part of the raised heath, occupied by typical heath plants, together with *Annophila arenaria* more deeply rooted in the less acid



Phot. 4. Hummocks of *Erica* and *Calluna* on a sandy part of the heath. Erosion here is due to the action of rabbits and wind. Recolonisation has commenced. In the background is a sand-hill on which *Annophila* persists, and on to which *Pteridium* is encroaching from the cultivated land behind.



Phot. 6. *Ulex Gallii* and *Erica cinerea* growing on the inland part of the heath. Plants here also include *Calluna*, *Carex*





## 3. THE VEGETATION OF THE RAISED BEACH.

A. *Dry types.*(a) *Heath proper.*

The major portion of the raised beach is at present occupied by a heath, and this is known locally as the Ayreland. This heath is undoubtedly primitive, though it may have been the seaward fringe of a formerly more extensive heath, said to have covered the northern part of the Isle of Man. Old inhabitants of Bride, and other villages in the vicinity, whose ancestors have lived in the neighbourhood for generations, describe the uplands as formerly a heath "just like the Ayre," of which the better parts were cultivated, the inhabitants spending some of their time in agricultural pursuits, and the remainder in fishing.

The soil of the main part of the Ayre is coarse, being, as mentioned previously, composed of pebbles of various sizes, together with a small proportion of blown sand. The landward fringe of this region bears a thin mantle of blown sand, which represents, in all probability, the remains of a line of low dunes of a former shore, part of this now being agricultural land.

At the present time, there is little indication of the extent of the heath in former times, except that isolated areas of heather and gorse occur at certain parts of the Bride hills, and these are frequently close to areas covered with bracken.

Whether the occurrence here of bracken indicates a former woodland, as has been suggested (11), or whether the Bride flora represents a relic of a more extensive primitive heath, is debatable. It is of interest to note that, at the present time, there is no natural or semi-natural woodland in the north of the Isle of Man. Feltham (5) mentions the barren aspect of the island in 1798, due to the lack of trees.

Evidence based on fossil pollen from the post-Pleistocene deposits in the Curraghs (4) suggests that the climatic conditions prevailing during the deposition of peat in that region were sub-arctic, and that forests at that time must have been either absent or scanty. Fossil birch pine and oak have been found, however, in the higher strata of the post-Pleistocene peat of the Curraghs, and this may suggest the possibility of a former extensive woodland, degenerating into heath over the north of the Isle of Man, the surviving trees in the west being ultimately destroyed by a rise in the water level following a flooding of the Curraghs, which are now at sea-level.

An interesting member of the heath flora of the Ayre is *Usnea articulata* which, though usually corticolous, is here saxicolous, and may suggest a relic of a woodland flora.

Trees can thrive in the vicinity, as is evidenced by the fact that planted species of elm, ash, sycamore and *Cordyline* flourish round all the farmsteads, some within several hundred yards of the Ayre; these trees are all less than 100 years old and have made good growth.

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The heath is an edaphic community, having developed on that part of the raised beach which has accumulated a fair proportion of organic matter, mainly present in the form of dry peat ("Troekentorf"), the percentage in some cases being as high as 13.49. Such regions are also definitely acid in their soil reaction ( $pH$  5.8-6.6) and devoid of any carbonate fraction.

The dominant plants are *Calluna vulgaris* and *Erica cinerea* which form a more or less complete covering in most cases, being accompanied by many typical heath species, along with some members of the flora of the consolidated dune slope.

Facies of *Ulex gallii* are a feature of certain parts of the heath, especially on slight sandy rises which are exposed to the predominant westerly winds, i.e. in places associated with a fairly rapid water loss.

*Carex arenaria* occasionally forms local societies, but these are generally the sites of former clearings, and in due course will become dominated by normal heath species.

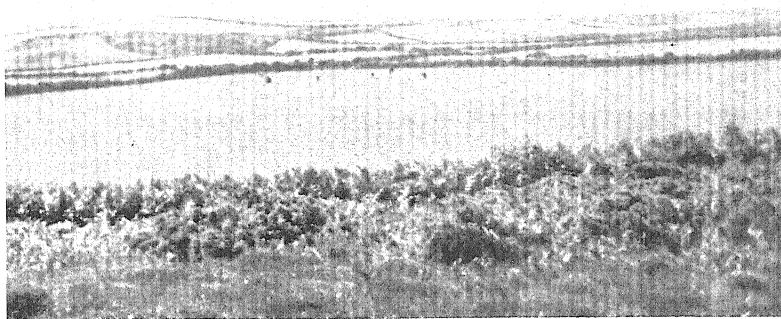
As has previously been suggested, there is a possibility of the heath having developed on an eroded maritime dune formation, the heath plants appearing after leaching and the accumulation of humus had produced a suitable soil. This view is supported to some extent by the occurrence on the heath of areas dominated by *Ammophila arenaria*.

The species of the heath flora consist of the following:

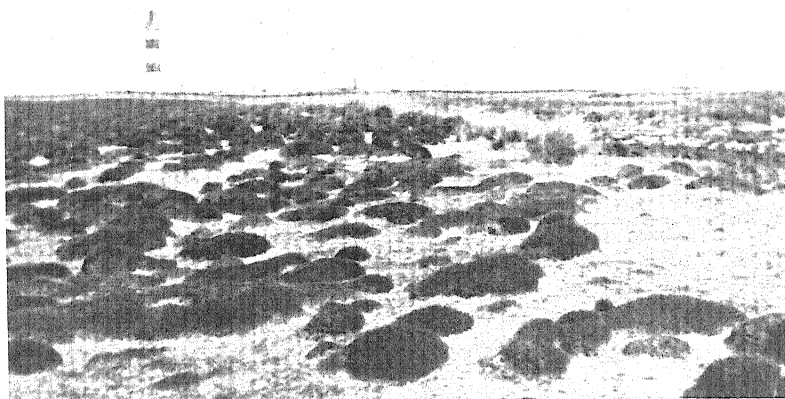
	<i>Calluna vulgaris</i>	} co-dominant	
	<i>Erica cinerea</i>		
<i>Viola canina</i> var. <i>ericetorum</i>	o.	<i>Hypochaeris radicata</i>	o.
<i>Polygala vulgaris</i>	r.	<i>Jasione montana</i>	f.
<i>Silene maritima</i>	o.	<i>Campanula rotundifolia</i>	o.
<i>Erodium cicutarium</i>	o.	<i>Erythraea centaurium</i>	r.
<i>Ulex gallii</i>	l.dom.	<i>Thymus serpyllum</i>	f.
<i>Ononis repens</i>	f.	<i>Teucrium scorodonia</i>	l.a.
<i>Lotus corniculatus</i>	l.a.	<i>Carex arenaria</i>	l.a.
<i>Rosa spinosissima</i>	l.a.	<i>Agrostis</i> sp.	f.
<i>Senecio jacobaea</i>	o.	<i>Ammophila arenaria</i>	l.
<i>Carduus tenuiflorus</i>	o.	<i>Deschampsia flexuosa</i>	f.
<i>Hieracium pilosella</i>	o.	<i>Festuca ovina</i>	f.
<i>Scilla verna</i>	l.	<i>F. rubra</i>	f.

The following cryptogams also occur:

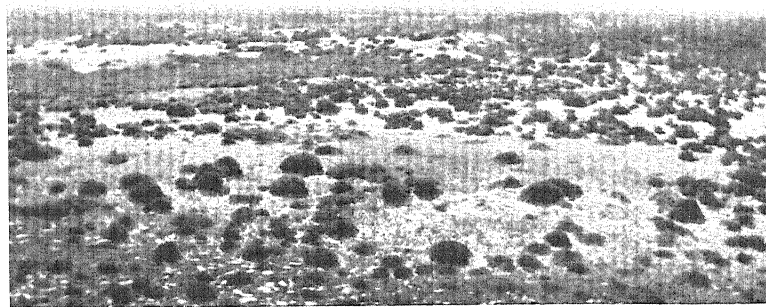
<i>Mosses.</i>	<i>Dicranum scoparium</i> var. <i>spadiceum</i>	o.
	<i>Hypnum cupressiforme</i>	o.
	<i>Polytrichum juniperinum</i>	l.
	<i>P. strictum</i>	l.
<i>Lichens.</i>	<i>Usnea hirta</i>	o.
	<i>U. articulata</i>	r.
	<i>Cladonia cervicornis</i>	l.
	<i>C. rangiformis</i>	o.
<i>Fungi.</i>	<i>Lycoperdon caelatum</i>	l.



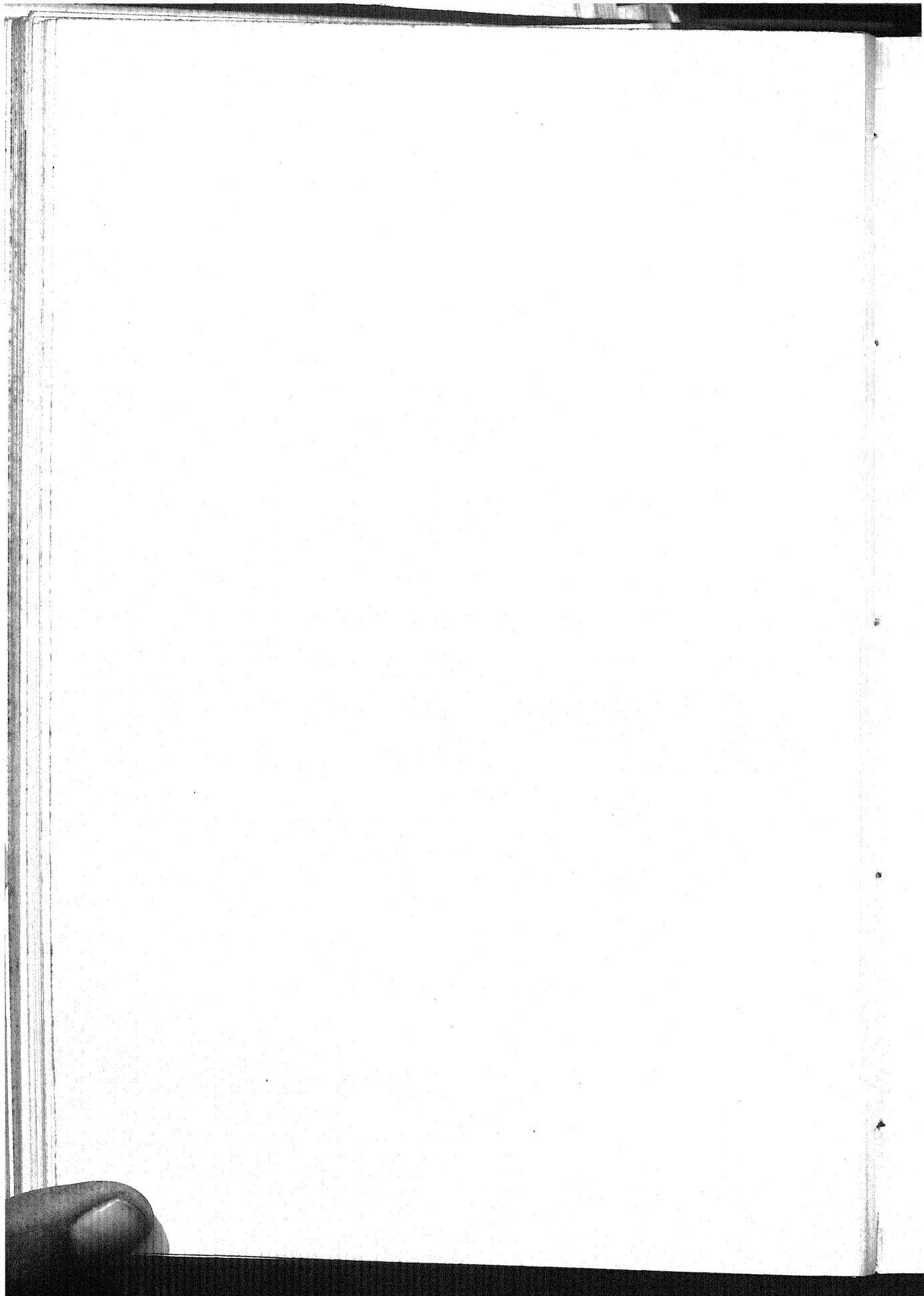
Phot. 8. View taken from a rise on the inland fringe of the present heath, looking over the agricultural land which was formerly part of it. The line of hills in the background is the ancient cliff of glacial drift marking the limits of the former shore. The typical hedges, occupied by *Ulex europaeus*, are a prominent feature. Note the spread of gorse and bracken from the hedge on to the heath.



Phot. 9. "Hummock heath" near the Point of Ayre lighthouse, on a part of the raised beach in the path of blown sand removed across the heath. The hummocks are mainly built up by young plants of *Erica* and *Calluna* which accumulate the sand between their branches.



Phot. 10. View of the "hummock" type of heath, occupying a pebbly part of the raised beach. Recolonisation is in progress, mosses, lichens, *Sedum* and *Thymus* being found on the clearings between the hummocks.



(a i) *Secondary succession following burning.*

Occasionally small areas of heath are accidentally burnt, and the surface vegetation is completely removed. Where this has occurred the regeneration of the heath has been fairly rapid. Those plants, such as *Ulex* and *Pteridium* (an invader) with deeper-seated rooting systems, recover by vegetative means, and many of the herbaceous species reappear from seed. The plants that suffer most are the dominants, as they have a woody system that burns well, but are not particularly deep rooted. They cannot recover easily, as, from observations made in several burnt areas, it is found that both *Erica* and *Calluna* are not readily stimulated to produce adventitious shoots.

The period that elapses between burning and regeneration varies according to the soil character, but where the soil is more sandy the seedlings of *Erica* and *Calluna* appear in the third or fourth year, after the soil has lost the ash added by burning and has passed to the acid state. Other heath species occur as soon after burning as conditions suitable for the germination of seed obtain.

(a ii) *Secondary succession following rabbit activities.*

"Hummock" heath. The occurrence of the "hummock" form of heath is mainly due to rabbit attack. Rabbits nibble the larger plants of *Calluna* and *Erica*, and also clear out spaces between the plants by frequent scraping. Such activities may have kept the heath in a state of flux over a long period.

Once scraping has exposed the underlying soil, the wind removes the surface soil, so that large bare areas may be formed. These bare areas are generally recolonised by the neighbouring plants, in a succession very similar to that described in the case of the consolidated dune slope, viz.:

- (i) Lichen stage.
- (ii) Moss stage.
- (iii) *Rosa spinosissima* stage (on sandy soil).
- Or (iii a) *Sedum*—*Thymus*—*Jasione* stage (on pebbly soil).
- (iv) Grass heath.
- (v) Normal *Calluna*—*Erica* heath.

(i) The bare areas of the raised beach usually show a coarser type of soil than that of the dune slope, and large pebbles are frequently a feature. The larger pebbles may become occupied by crustaceous lichens, such as *Lecanora*, though their presence does not assist the succeeding colonists.

The earliest colonists which prepare the soil are the lichens *Cladonia cervicornis* and *Parmelia physodes*, which grow at a comparatively rapid rate and furnish a scanty humus on becoming scorched up in the summer.

(ii) The preparation of the soil by lichens enables the spores of the moss *Polytrichum juniperinum* to develop, though in several instances this plant was found to be the primary invader of the clearing. At first, *P. juniperinum* occurs in pure patches, but is soon followed by other mosses of the heath flora, such as *P. strictum*, *Dicranum scoparium* var. *spadiceum* and occasionally



*Hypnum cupressiforme*, and these ultimately survive in patches after the clearing has become covered with other vegetation.

(iii) In those clearings where the soil is more sandy, the earliest phanerogam to appear is frequently *Rosa spinosissima*, developing both from seed, and by means of long suckers which serve to enable it to gain the more open parts of the clearing from the fringe of vegetation bounding it.

In several cases this plant has also served to cover over the coarser clearings, as it acts as an efficient sand-binder so long as the amount of blown sand is not too great.

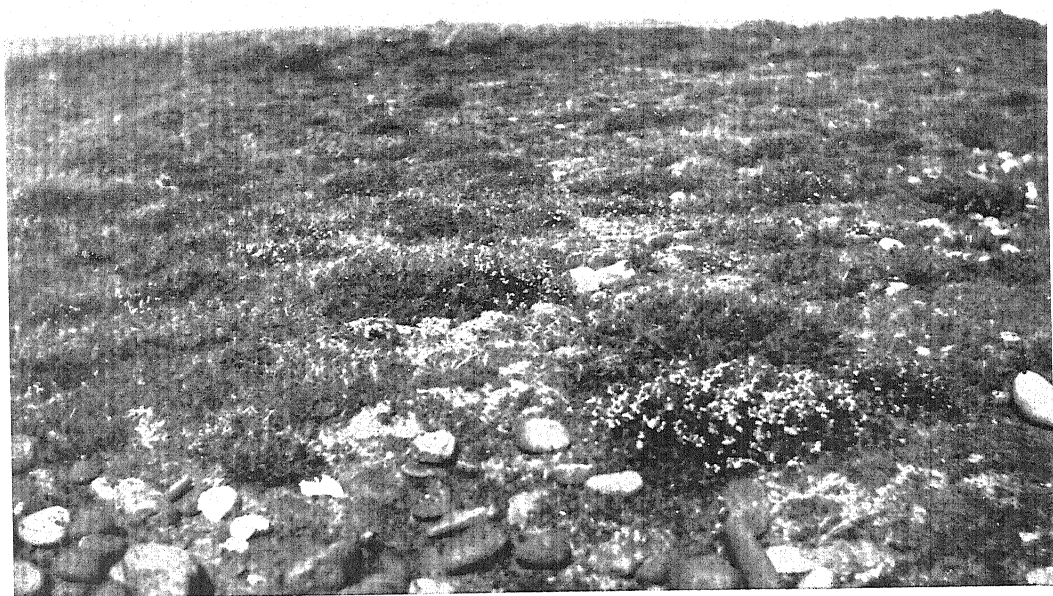
(iii a) Where the soil of the clearing is more pebbly the earliest phanerogam to appear is *Sedum anglicum* which is in a dwarf state and spreads rapidly, both by vegetative means and from seed, young plants forming a striking feature of the clearings owing to the contrast of their reddish tinge against the light coloured soil. *Sedum* is soon followed by *Thymus serpyllum* and *Jasione montana*, both of which flower and fruit freely.

(iv) The mosses and early phanerogams serve to make the soil more suitable for other species, which include *Carex arenaria* and those grasses common to sandy heaths, such as *Festuca* spp., *Deschampsia* and *Agrostis*. Once these grasses enter the zone, the bare area is soon obliterated and a turf is developed in which many of the normal heath plants occur, including *Viola canina*, *Lotus corniculatus*, *Erodium cicutarium*, *Ononis repens*, and *Galium verum*, as well as the heath dominants. The more extensive clearings remain in the grass-heath stage until complete leaching and a larger accumulation of humus have occurred.

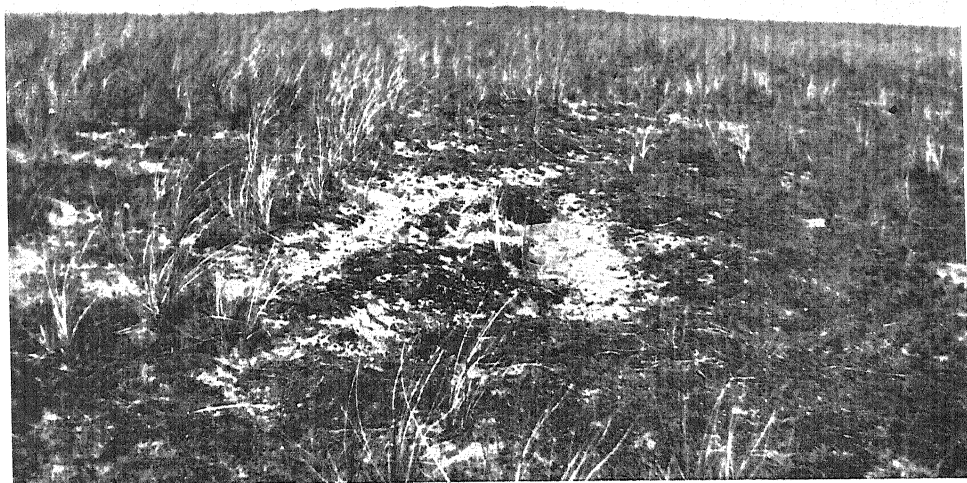
(v) Finally, the dominants, *Calluna* and *Erica*, take charge of the area, which then becomes typical heath.

Mention must be made here of a variation in the succession sometimes noticed, especially in rather deep clearings. After the early stages (i) and (ii) have commenced, seedlings of *Erica* and *Calluna* are found occurring along with a sparse growth of lichens and mosses. This may be connected with the soil reaction (which may be affected by lichen acids) for that of two such clearings was found to be relatively acid, viz. pH 5.8. The young *Erica* and *Calluna* plants gradually accumulate sand particles and plant debris, and spread outwards and upwards to form small hummocks, which also become occupied by lichens, mosses, and the colonising phanerogams. The bare parts of the clearing generally follow the usual succession, but by the time the soil is covered with vegetation the dominant plants are in control, so that the clearing does not pass through a grass-heath stage.

It thus comes about that "hummock" heath is partly retrogressive, the hummocks being "islands" left by biotic attack, but parts may be progressive, the hummocks being accumulations of blown sand built up from the level by heath plants. In many cases the two types of hummock occur together.



Phot. 11. Near view of a late stage of the recolonisation of "hummock heath." The low-growing plants of *Sedum*, *Thymus* and *Lotus* are stabilising the small amount of blown sand, and the smaller plants of *Erica* and *Calluna* are spreading outwards.



Phot. 12. The landward slope of the dune bank at Ballaghennie. It is occupied by *Ammophila* and various sward-forming plants such as *Thymus serpyllum*, *Galium verum*, *Festuca* spp., *Lotus corniculatus*, *Sedum anglicum*, etc. Occasional plants of *Brassica monensis* and *Eryngium* occur. Note the cleared areas caused by the scraping of rabbits and the action of the wind.

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(b) *Community of Ammophila arenaria on hummocks.*

At certain parts of the Ayre, some distance inland from the sea and separated from the maritime fringes of blown sand by the heath, low sand hills occur which are characterised by the predominance of *Ammophila arenaria*. These rises, in all probability, represent former dunes, and appear to be a survival of an ancient system, as they are roughly in lines parallel to the present shore.

In several cases the hills are occupied by a community similar in floristic composition to that of a typical "grey dune," and bear, besides *Ammophila*, *Festuca rubra*, *F. ovina*, *Jasione montana*, *Sedum anglicum*, *Galium verum*, *Rosa spinosissima*, *Hypnum*, and *Peltigera*.

In other cases, where the hummock is only 3 or 4 feet above the surrounding heath, the vegetation consists of heath plants, including *Calluna*, *Erica* and *Ulex gallii*, amongst which tufts of *Ammophila* occur in fair profusion.

It seems that these hummocks are relict, and that heath plants replace the former vegetation as leaching proceeds and as humus collects, the deeper-seated *Ammophila* continuing to grow in the more alkaline subsoil.

(c) "*Creggans*"—communities of *Ulex europaeus*.

At the inland margin of the heath, where it adjoins the agricultural land, there are certain sand-hills occupied by *Ulex europaeus*, these being known locally as "creggans." Some of these "creggans" are, very likely, former dunes, but others appear to be constructions of Neolithic man, who frequently used the abundant blown sand of this region in the construction of "barrows."

The common gorse, here, as opposed to *Ulex gallii*, is an invader on the heath, and undoubtedly owes its occurrence to human activities. It is a practice, in Manx agriculture, to construct stout hedges of stones and turf, and to plant *Ulex europaeus* on them. Such hedges were made when parts of the heath were reclaimed for cultivation, and it is from these hedges that the gorse has encroached on to the heath. The gorse forms fairly pure communities, and is subduing the legitimate heath plants owing to the shade produced and because of its immunity from rabbit attack. In those "creggans" examined, the surface soil has a marked acid reaction, viz. pH 5.8, but it is possible that as there is a deep sandy soil the gorse is thriving in a more alkaline subsoil by deep rooting; this fact also may be a factor limiting its spread to the main part of the heath. Underneath the gorse bushes the flora consists of *Erica*, *Calluna*, *Carex*, *Festuca*, *Lotus* and other heath species, but the large plants are in a sickly condition.

(d) *Bracken communities.*

*Pteridium aquilinum* is another invader on the heath, and it, too, probably owes its presence to human interference. The main bracken communities

occur in the same vicinity as the gorse, in some cases invading the "creggans" and stifling all other inhabitants.

The bracken is invading the heath from the arable land, where certain fields of permanent pasture are very badly infested. The nearest points to the Ayre which bear bracken are localities where Boulder Clay (locally called "marl") is found. During the reclamation of parts of the former heath, "marl" was carted to the fields and ploughed in after the surface vegetation had been cleared. There is a possibility, therefore, that the bracken was introduced with the Boulder Clay, and thus spread in those fields which were put to permanent pasture, whilst in others it was kept in subjection by normal cultivation. It is from the infested fields that the bracken has spread on to the heath, especially at the more sandy points. It is being kept in check, apparently, by the nature of the soil on the main part of the heath, though *Pteridium* does not readily invade mature heath unless assisted by the occurrence of fires.

#### B. *Damp types.*

Mention has been made of the ditch which drains on to the Ayre from Lough Cranstal, causing considerable "flushing" during the winter months.

Lough Cranstal is a small lake, occupying a large depression in the glacial drift, receiving water from several springs, and the drainage water from the Bride Hills.

It can be gathered from old maps and deeds that the lake was formerly of a greater extent than at the present, and the amount of surplus water would also have been larger than it now is.

At the present time, the "lough" bears an aquatic formation, approaching the fen type in the less deep portions, and becoming a marsh at the margins. The overflow from the "lough," owing to the natural configuration of the area, drains towards the Ayre. The drainage channel, which originally must have been a small stream, has been artificially extended at some former time to produce a shallow ditch, which leads water on to the Ayre at a point about 400 yards from the sea.

The amount of water coming down this ditch is fairly large during the winter, when it lies on the surface of the soil at the mouth, forming a shallow pool about 160 yards long and 20 yards wide. This water percolates through the sandy soil and gradually disappears, so that in the summer months, when little or no water leaves Lough Cranstal by the ditch, the former flooded region appears as a green area, bearing the vegetation of neutral grassland and clearly demarcated from the heath which surrounds it, owing to its colour and in the striking absence of heath plants.

The neutral grassland and the drainage channel will be considered separately.



(e) *Neutral grassland.*

The area flooded in the winter months occupies a rich black sandy soil with an organic fraction ("loss on ignition") as high as 12.93 per cent. Diggings in this region give evidence of a time when the ditch brought down large quantities of mud and silt, as a compacted layer of this material is found at a depth of 6 inches below the present surface.

The soil reaction is alkaline (pH 7.6), and the organic matter is thoroughly decayed and well mixed with the mineral fraction to a depth of from 10 to 14 inches. The drainage water serves to neutralise the acids of decay, etc., but, also, its alkaline nature and the aeration it affords must cause a greater activity of the soil bacteria.

The vegetation of the drainage area consists mainly of grasses and other plants characteristic of pasture land, along with which are several weeds of cultivation. The region is extensively grazed by rabbits and sheep, which are instrumental in keeping the richer vegetation in subjection, so that, during the summer, the vegetation forms a close-cropped sward. A member of the flora which is characteristic of sandy soils, is *Plantago coronopus*, which is conspicuous at the margin of the community in the summer months, when the grasses become somewhat dried up.

At the margin of the region, where the influence of drainage water becomes less marked, the soil reaction is about neutral, the organic fraction being much less than that of the main part of the inundation area, in this case forming a shallow surface layer. Here some of the heath species, such as *Thymus*, *Lotus*, *Rosa*, *Ononis*, and *Festuca*, occur along with the grasses of the central part.

Species occurring in the region are the following:

*Lolium sp.		} co-dominant	
*Poa sp.			
*Agrostis sp.			
Anthoxanthum odoratum			
*Bromus sp.	f.	Galium verum	o.
Ranunculus acris	f.	Achillea millefolium	f.
Ranunculus bulbosus	o.	Senecio jacobaea	o.
Althaea officinalis	o.	Cnicus lanceolatus	o.
Ononis repens	o.	Euphrasia sp.	o.
Trifolium repens	f.	Thymus serpyllum	o.
Lotus corniculatus	l.a.	Plantago coronopus	a.
Potentilla anserina	o.	Polygonum aviculare	f.
Rosa spinosissima	o.	Rumex sp.	o.
Conopodium majus	f.	Urtica dioica	l.

\* Species not certain, owing to grazing.

(f) *Ditch from Lough Cranstal.*

The lower part of the ditch from Lough Cranstal can be considered as part of the raised beach, as it has been cut out from it and its sides are composed of the sand and pebbles excavated during its construction.



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The sandy banks can be included with the heath, as they are occupied by heath species, invaded here and there by *Ulex europaeus*, and occasionally bearing species common to maritime sands, such as *Ammophila*, *Cerastium semidecandrum* and *Festuca rubra*.

The vegetation of the ditch itself passes from neutral grassland, at the mouth, to a damper type, which is practically that of a marsh. The soil at the higher level contains a greater proportion of silt than the lower part, and is of a heavier type. The amount of water varies with the season, but, on the whole, the ditch receives and retains more water than the "drainage plain" on the Ayre. The bottom of the ditch is occupied by grasses of damp meadowland, along with which are certain marsh species. The vegetation, in a normal year, remains fresh in appearance throughout the summer.

A list of species noted in this region is as follows:

<i>Anthoxanthum odoratum</i>	l.a.	<i>Angelica sylvestris</i>	o.
<i>Alopecurus pratensis</i>	a.	<i>Veronica chamaedrys</i>	l.a.
<i>Phleum pratense</i>	f.	<i>Lamium album</i>	f.
<i>Poa</i> sp.	f.	<i>Plantago lanceolata</i>	o.
<i>Catabrosa aquatica</i>	l.a.	<i>Urtica dioica</i>	l.a.
<i>Ranunculus flammula</i>	o.	<i>Carex</i> spp.	f.
<i>Cardamine pratensis</i>	f.	<i>Equisetum sylvaticum</i>	o.
<i>Potentilla anserina</i>	o.		

### 4. THE REGION OF ARABLE LAND.

The agricultural land of the raised beach consists of a zone of varying depth, forming the landward fringe of the heath, and extending almost up to the present eastern beach, and some small plots of land at the Point of Ayre lighthouse.

Until the nineteenth century Manx agriculture appears to have been of a very primitive kind. This was due to a variety of circumstances, amongst which were (1) the insecurity of tenure of those working on the land, (2) the lack of fences and hedges, (3) the absence of any attempt to improve the nature of the land by tilth and manuring, and (4) the lack of suitable drainage systems.

Up to 1665 fences were built only for use during the summer, so that in the winter the land became common, and thus, uncared for. After that date fences were ordered to be left standing during the winter, the height and nature being stipulated, so that there was some incentive to grow those crops which would now thrive with the extra protection afforded.

During the period 1735 to 1845 attempts were made, mainly by Bishop Wilson, to instil some agricultural ideas into the natives, and, to some extent, these were successful, many subsequent improvements being associated with that period. Woods (13), writing in 1811, describes a simple five-year rotation

of crops in use in parts of the island. This consisted of the following sequence:

- 1st year. Potatoes or turnips, in well-manured soil.
- 2nd year. Barley.
- 3rd year. Clover.
- 4th year. Oats.
- 5th year. Peas or oats.

In poor soils, fields were frequently allowed to stock themselves with natural grasses after three or four rotations, and some of these fields never came under tilth again.

In 1817, the development of intensive cultivation received a set-back, in the form of a successful attempt to levy a tithe on crops of turnips and potatoes, both recent introductions to the island, and not until fairly recent times was there a recovery.

The region under survey forms part of the parish of Bride, which, as an agricultural area, is of comparatively recent development, for early in the nineteenth century, farming was carried on only as a part-time occupation, the men being largely employed in fishing during the summer and autumn months to supplement the livelihood gained from the land.

As late as 1845 very primitive methods of agriculture were in use in the north of the island, manure being carried to the land in creels, so that only the more accessible and profitable pieces of land were cultivated (10). Shortly after this, however, scientific treatment of the land was being encouraged by the Government, and draining and manuring were undertaken. In Bride, the lighter sandy soils of the drift plain were improved by ploughing in marl, obtained from the abundant local deposits of Boulder Clay, which contained (according to Cumming (3)) from 2 to 5 per cent. of lime.

Prior to this time, as mentioned in a previous section, the Ayreland heath was of greater extent than now, reaching, in some places, up to the foot of the old cliffs of glacial drift, but parts of it soon came under the same treatment as the other land of the parish, and, ultimately, were added to the arable land. In 1861 the heath was divided up into strips and sold by the Crown. Many of the fields, indicated on the Ordnance map as fringing the present heath, date from that time, as those farmers who acquired the land hedged off portions and commenced active destruction of the heath vegetation. The heath plants were hacked off, and "marl," seaweed, and farmyard manure were ploughed in, and attempts were made to raise crops. At first only grass was grown, but this was followed after several years by potatoes, and ultimately some of the fields were treated as part of a rotation which is in use at the present time, and which seems to be a modification of the one described by Woods.

The present rotation is as follows:

1st year. Turnips or potatoes.

2nd year. Corn (oats, wheat or barley) sown with which are grasses and clover, forming an undergrowth. Top dressing follows harvesting.

3rd year. Hay—raised from grasses and clover of the previous year.

4th year. Fallow.

5th year. Corn—followed by manuring after the harvest.

Some of the reclaimed land is still treated in this way, but a number of fields have been allowed to become permanent pasture and are grazed by sheep. Several of the neglected fields bear extensive areas of bracken, which has advanced on to the heath at certain places.

At the lighthouse the small plots of land used as kitchen gardens were reclaimed from the heath over 100 years ago and were improved by digging in seaweed and household refuse, including ashes, largely from wood fires. The soil in these plots is quite rich and raises very decent crops, despite the exposed situation.

The cultivated fringe of the former heath is now in a state of quiescence and no further attempts to extend the zone of cultivation seem likely; in those cases where tilth has been stopped it seems possible that the land will revert to a heath once more, though this may be prevented by the extensive growth of bracken which has taken control of permanent pasture at several points.

#### SUMMARY.

1. The Ayreland occupies a former shore, composed mainly of large pebbles, but also bearing a certain amount of blown sand locally distributed.

2. The vegetation of the main part of this raised beach consists of heath-land, dominated by *Erica cinerea* and *Calluna vulgaris*, which has developed as organic matter accumulated and the soil became acid. Rabbit activities have served to produce a "hummock" heath at certain places, which passes back to normal heath as the clearings are re-colonised.

3. Certain sand hills on the Ayre are dominated by *Ammophila arenaria*, which also occurs in the modified dune formation on the seaward fringe of the raised beach. The inland *Ammophila* hummocks may represent the relics of a former dune system which has become eroded, so making the soil conditions suitable for the development of heath.

4. Communities of *Pteridium aquilinum* and *Ulex europaeus* invade the heath from the bounding arable land, and may owe their presence to human activities.

5. The inland margin of the raised beach has been cultivated in the last 100 years, having been reclaimed from the heath which formerly occupied it.

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## APPENDIX.

## SOIL CHARACTERS.

During the summer of 1929 a series of soil samples was taken from various points on the Ayre. As the whole of the Ayreland occupies the same geological formation, the samples were taken from areas showing some particular type or phase of vegetation, and in all cases contained a large proportion of sand, as it is only in places where this has accumulated that vegetation has been able to develop.

As the soil in all cases was either of a very loose nature, or had a layer of large pebbles at or near the surface, no soil borer was found to be of any use in gathering samples. The samples were obtained by digging with a flat trowel, taking soil from an area 3 inches square and to a depth of 6 inches, this depth being found to include the majority of the root systems examined; below this depth the soil was, in practically every case, completely mineral in origin.

The organic fraction of the soil was obtained by finding the loss of weight on ignition, the initial weight being that of the samples heated to 100° C.

The soil reaction was ascertained by means of a "B.D.H. Capillator Outfit"; 10 gm. of soil were mixed with 25 c.c. of distilled water and the whole shaken in a mechanical shaker for 15 minutes, after which the mixture was centrifuged and the clear liquid tested with the indicator. The indicators used were brom-thymol blue, cresol red and brom-cresol purple, the two latter being used as a check on the former for alkaline and acid ranges respectively.

The soil carbonates were measured by obtaining the loss of weight, due to CO<sub>2</sub> evolved, on treating the soil with hydrochloric acid in a Schrötter apparatus, which was first standardised with several samples of marble which were taken to be pure calcium carbonate.

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Mechanical analyses of three samples were made, the details being as follows, the figures representing percentages by weight:

Locality	Coarse sand	Fine sand	Silt	Clay	Organic matter
Embryo dune ...	96.1	0.3	0.1	0.7	0.86
Heath at Ballaghennie ...	76.5	2.6	0.8	0.5	13.49
Hummock of heath plants	92.2	0.4	0.2	0.1	5.55

The general results show that the Ayreland heath is developed on a dry soil, poor in carbonates and having an acid reaction. The acid reaction is to be correlated with the accumulation of organic matter as vegetation develops, but a marked contrast is offered by the "flush" due to the drainage water from Lough Cranstal collecting on the Ayre. In this area, although the amount of organic matter is high, the soil reaction is alkaline and can be explained by the mineral matter in the drainage water and by the greater aeration produced in the soil.

The conditions met with in passing from shore sand to the stabilised soils bearing heath are very similar to those found in passing from the bare soil of a clearing to the stable soil of the recolonised clearing.

The results are summarised below, all figures representing percentages:

(a) *Bare soils.*

Locality	pH	Humus (loss on ignition)	Car-bonates	Water
Embryo dune ...	7.6	0.86	2.73*	0.10
Clearing in consolidated dune bank	6.9-7.0	1.69	0.98	—
Clearing in hummock heath ...	6.8-7.0	0.82	0.36	—

(b) *Soils with sparse vegetation.*

Seaward face of dune bank ...	6.9	Nil	3.32*	—
Clearing in heath occupied by lichens	5.8	1.02	Nil	—
Clearing in heath occupied by mosses	6.0	1.47	0.07	—
Clearing in heath occupied by <i>Rosa spinosissima</i>	6.7-6.8	1.11	Nil	—

(c) *Soils with a covering of vegetation.*

Consolidated dune bank	7.0	1.24	0.75	0.18
Heath at Ballaghennie	6.4	13.49	Nil	9.2
Heath at point of Ayre†	5.8	10.86	0.04	6.4
Grass heath	6.4	5.54	Nil	—
Hummock of heath plants at Ballaghennie	6.6	5.55	Nil	—
Hummock of heath plants at point of Ayre†	6.3	4.57	0.41	2.04
Recolonised hummock zone...	6.5	2.17	Nil	—
Gorse "Creggan"	5.8	9.6	Nil	4.0
Inland hummock with <i>Ammophila</i>	6.4	7.46	Nil	—

(d) *Neutral grassland.*

Centre of drainage area	7.6	12.93	0.02	—
Margin of area, adjoining heath	6.9	3.24	Nil	—

(e) *Cultivated grassland.*

Grassland with <i>Pteridium</i> : (a) surface	6.6	4.40	Nil	—
(b) rhizome level	6.4	1.00	Nil	—
Grassland free from <i>Pteridium</i>	6.9	2.19	Nil	—
Pasture at Cranstal	6.8	2.67	Nil	—

\* Mainly in the form of shell fragments. † In path of blown sand removed across the heath

# PRELIMINARY OBSERVATIONS ON SCOTTISH BEECHWOODS. INTRODUCTION AND PART I

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(With one Figure in the Text.)

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## INTRODUCTION.

THE study of Scottish beechwoods, begun some years ago, was suspended because no satisfactory account of their relationships to other types of vegetation could be given until more was known about the natural and semi-natural plant communities. As a result, however, of the discussion on beechwoods at the International Botanical Congress (Cambridge, 1930), it was considered desirable to have the existing information written up at once. Hence this preliminary account lays no claim to completeness, and the data employed are practically restricted to the north-east of Scotland and more particularly to the neighbourhood of Aberdeen.

### THE INTRODUCTION AND SUBSEQUENT HISTORY OF THE BEECH.

Although beech (*Fagus silvatica*) is not considered native to Scotland, its behaviour as set forth in this paper justifies the conclusion that this tree is growing within its climatic limits and has, under existing conditions, become established as a successful competitor with the native flora.

Historical evidence on the introduction of beech seems to be based on Walker's observations. In view of Loudon's (13) incorrect reproduction of these, it may be well to quote Walker in full. After giving measurements of



five large beech trees, he says: "The beech was not copiously planted in Scotland, till a little before and after the Revolution; and the trees planted about that period do now form in many places, considerable timber, as at Inveraray, Arniston, Hopetoun House and elsewhere. But the four trees last mentioned, which appear to be nearly contemporary, are of a much more remote aera. They seemed to have been planted single and merely as a curious foreign tree, in the garden of some eminent person. From their dimensions and manner of growth, they may be presumed, at least, to have been planted between the years 1540 and 1560. So that they may now be estimated at between 240 and 260 years old. From the state of the Ormiston Hall, and Newbottle tree (two of the five measured trees) it may be concluded, that the beech, if it meets with no accident, will grow with sound timber, for at least 250 years (24)." If Walker is correct the beech was a rare tree in Scotland in the middle of the sixteenth century, and was "copiously planted" a century later. By the beginning of the nineteenth century experience of the beech must have been fairly extensive, for Sinclair writes: the beech "thrives well in a deep and sandy loam: it will even grow to a great magnitude among the rocks of the Highlands, where soil is hardly visible. It is not reckoned proper to intermix it with plantations of oak and other timber: for being a quick grower, and extending its roots to a distance, it overtops and starves its neighbours (19)." At that time good beech timber in Ross and Cromarty fetched 4s. per cubic foot and in some other parts of the country from 6d. to 4s. In 1843 Dickie writes: "This tree is rather general in Aberdeenshire," and "From the accompanying table it will be evident that this county presents, in many parts, a soil and climate favourable to the growth of this tree (2)." About this time beech timber "never attains a high price, and is often a drug in the market (6)." Finally the testimony of the late Prof. Trail, whose knowledge of the local flora was unrivalled, may be given: "Denizen: long cultivated in Scotland, and freely self-sown... This is one of the most plentiful trees of the lower levels, so readily self-sown and so fertile that it looks native in many places (21)."

The discovery by Erdtman (3) of beech pollen in the Post-Glacial peat of Lewis, Orkney and Shetland has suggested the nativity of beech, but the evidence rests upon one pollen grain from each locality—evidence too slender to be accepted without further support. Two of the pollen grains (details of the third are lacking) were found under conditions which do not prevent the possibility that the grains came from introduced trees. Also, if the indigenous occurrence of pine in Shetland must be left unsolved owing to the possibility of wind carriage of pollen over considerable distances and to the absence of confirmatory evidence from fossil macro-remains, this applies with equal force to the beech, no fossil macro-remains of which have so far been discovered in Scotland. At present, therefore, the balance of evidence is in favour of considering the beech alien to the Scottish flora.

The evidence summarised above shows that the beech was widely planted in Scotland. Apart from the use of beech as an ornamental tree, the value of the timber at the beginning of last century may have been an inducement to plant, and the subsequent fall in value a reason for the survival of many plantations of old trees. But the study of the distribution of these is at once an argument in favour of its artificial spread and a clue to its widespread acceptance. In the main beech is found associated with cultivation, and as we ascend the river valleys it rapidly diminishes in frequency and is replaced by indigenous trees. In the lowlands of north-east Scotland generally and particularly near Aberdeen, the prevalence of beech may be considered an expression of the scarcity of native woods and of the need for shelter, for the beech is found chiefly in those places where plantations of trees would afford shelter to crops and stock. Its suitability for this purpose is due to the wind-resistant qualities of this tree (1, 27). These were apparently widely recognised over a century ago, for in many places beech forms the chief and sometimes the sole (surviving) constituent of shelterbelts formed for the protection of agricultural crops and plantations of less wind-resistant trees. It was also commonly planted as marginal trees to plantations of conifers, boundary trees to arable fields and for ornament and shelter in the neighbourhood of dwelling houses (20).

Beech has not been exclusively planted in such places but occurs on sheltered alluvial soil, steep slopes of "dens" and river banks where the flora is of a quite different type. The small number of these examined prohibits any attempt at statistical analysis, but a short account is given under the heading *Herbaceous Woods* (p. 154).

In the neighbourhood of arable cultivation beech has no opportunity of showing its behaviour towards other communities of plants, but where it adjoins woodlands its relationship to these can be studied. The subject matter is, therefore, treated in two parts, the first dealing with shelterbelts, a preliminary survey of which has been made, roughly from the Firth of Tay to the Dornoch Firth; the second with the relationship of the beech to woodland as shown in the neighbourhood of Aberdeen. Before proceeding a few general observations may be made.

#### THE CLIMATE OF NORTHERN SCOTLAND.

There are three well-marked "climates" in the north of Scotland: (1) the Aberdeenshire type, found typically in the promontories of north-east Aberdeenshire and Caithness, (2) the Morayshire type characteristic of the lowlands bordering the Moray Firth from Banff in the east, westwards to Beaully and north to Golspie, and (3) the West Highland type characteristic of the Western Highlands and Islands.

In all three the prevailing wind is westerly, but whereas a high rainfall occurs in the west (40 in. to over 100 in.—1016–2540 mm.) that on the sheltered

side of the Grampians is much less (near the coast 25–30 in., i.e. 635–762 mm.). The proportion falling during the six months, April–September, in the three representative stations, Aberdeen, Gordon Castle (Moray) and Fort William (west Inverness) is 46·42, 49·64 and 37·22 per cent. respectively.

Table I. *Total and monthly rainfalls at three stations representative of the three types of "climate."*<sup>1</sup>

		Aberdeen 57° 10' N.		Gordon Castle (Moray) 57° 37' N.		Fort William (W. Inverness) 56° 49' N.	
		in.	mm.	in.	mm.	in.	mm.
Jan.	...	2·18	55	2·02	51	9·63	245
Feb.	...	2·05	52	1·92	49	7·53	191
Mar.	...	2·41	61	2·32	59	6·84	174
April	...	1·87	48	1·75	45	4·47	114
May	...	2·33	59	2·12	54	3·99	102
June	...	1·71	43	2·04	52	3·58	91
July	...	2·81	71	3·20	81	4·83	123
Aug.	...	2·74	70	3·17	81	6·16	156
Sept.	...	2·22	56	2·50	64	6·32	160
Oct.	...	3·00	76	3·16	80	7·14	181
Nov.	...	2·95	75	2·88	73	8·16	207
Dec.	...	3·22	82	2·69	68	10·15	258
Totals	...	29·49	748	29·77	757	78·80	2002

The range of temperature is small and about the same in all three types. The data reveal high mean maxima and high mean minima for the west coast. Aberdeen shares the high minima of the west, but has relatively low maxima, particularly during May and June, whilst Moray combines high maxima with low minima. But the winters are mild in all three types.

Table II. *Mean monthly maximum and minimum temperatures (° F.)*<sup>2</sup>.

		Aberdeen		Gordon Castle (Moray)		Fort William (W. Inverness)		Braemar (Aberdeenshire, alt. 1120 ft.)	
		Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
Jan.	...	42·3	33·4	43·1	33·1	43·2	34·6	39·5	29·0
Feb.	...	43·2	33·4	44·3	32·9	43·6	34·0	40·1	28·6
Mar.	...	45·7	34·4	46·6	33·6	46·2	35·0	42·2	29·7
April	...	49·8	37·6	51·8	36·5	51·8	37·8	48·3	33·0
May	...	54·5	41·8	57·2	40·8	57·7	42·5	54·8	37·6
June	...	59·9	47·0	62·9	46·0	63·3	47·9	61·6	43·6
July	...	62·8	50·3	64·7	48·8	64·0	50·4	62·9	46·6
Aug.	...	62·4	49·9	64·2	48·6	62·9	50·3	61·3	45·8
Sept.	...	59·2	46·7	61·1	45·3	59·8	47·1	57·6	42·2
Oct.	...	52·8	41·7	53·9	40·2	53·0	41·9	50·0	37·0
Nov.	...	46·8	37·4	47·7	36·6	47·2	38·1	43·9	32·8
Dec.	...	42·9	34·2	43·5	33·6	44·1	35·2	40·2	29·3

Generally the west is mild, wet and windy, Moray is mild and dry with an early spring and early harvest, whilst the Aberdeen climate, with east winds prevailing during March, April and May (and often in June) with much coastal

<sup>1</sup> *Book of Normals*, Sect. 5, 1924.

<sup>2</sup> *Book of Normals*, Sect. 1.

fog has a cold late spring and because the summer temperature is low a late harvest<sup>1</sup>.

Wheat is grown in Moray and Easter Ross, but not in the West and very rarely in Aberdeenshire. *Quercus robur* and *Q. sessiliflora* set fertile seed in Moray but not near Aberdeen. Beech grows and sets seed in all three types. It does not, however, produce ripe fruit at Balmoral nor Braemar, where the maximum summer temperatures are relatively high but the spring minima are low (*v. data*). These low spring temperatures probably account for the inability of the beech to produce ripe seed.

#### THE BEECH AND LATITUDE.

As a planted tree, beech occurs in every county in northern Scotland, its vigour varying much according to soil and exposure to wind. It sets seed as far north as Caithness (lat. approx. 58° 30') and under the humid conditions of the west coast, for example, at Inverinate on the Kyle of Lochalsh in west Inverness-shire.

Subspontaneous beeches have been seen at Rosehall, in Sutherlandshire, and in Argyllshire, and doubtless occur elsewhere in the west. Beech regeneration is general along the east of Scotland.

In Scandinavia planted beech grows at lat. 67° 56' N. where it sets ripe seed (10).

#### THE BEECH AND ALTITUDE.

H. B. Watt records the beech at 1100 ft. (335 m.) at or near the village of Braemar in Upper Deeside (26). In the neighbouring valley of Strathdon the beech is growing near Allargue at an approximate elevation of 1350 ft. (411 m.) and at the village of Tomintoul at about 1150 ft. (350 m.). At both places the beech appears to be quite healthy but attains no great size.

The highest elevations at which reproduction has been observed are at Glendye (alt. 500 ft.—152 m.) and at Craig Castle (alt. 700 ft.—213 m.). Mr Edwards, forester at Balmoral (alt. 950 ft.—290 m.) informs me that he has seen no fertile seed there, although planted trees grow moderately well.

In Norway beech planted at 333 m. forms seed (11).

#### THE FORM AND HEIGHT GROWTH OF BEECH.

In several places the beech attains a height of over 90 ft. (27 m.), producing in canopy a long clean stem comparable to those on the South Downs. On the other hand, while the trees of some plantations do not much exceed 50 ft. (15 m.), in no observed examples do the trees assume the wind clipped bush forms such as are found on the exposed Jutland heaths, nor the crooked stems of the old beeches in Rold Skov in North Jutland (25). In Denmark racial

<sup>1</sup> This brief account of the climatic conditions is condensed from fuller information supplied through the instrumentality of Mr G. G. Esslemont, Aberdeen, whom I wish to thank for his kind assistance.

forms have been discovered (17), and opinion is divided how far on certain soils "bad forms" (*wrange bogen*) are inherent and how far caused by the environment. Here, however, there is little difference in the stem and crown form of the trees, and the differences in height attained are correlated with habitat differences.

Loudon (14) mentions a number of trees of 70–90 ft. (21–27 m.), and Hunter (9), trees from 100 ft. (30 m.) to "an entire height of 120 ft. (37 m.)." Trees of over 90 ft. (27 m.) are, however, exceptional and found only in favourable situations, the usual heights varying from 60 to 80 ft. (19–24 m.).

As the beech sets seed freely on the low ground, it is clear from the preceding data that the climate of the lowlands of the north of Scotland is quite suitable for beech growth and regeneration.

#### PART I. GRASSY (SHELTERBELT) AND HERBACEOUS BEECHWOODS.

##### GRASSY (SHELTERBELT) BEECHWOODS.

Belts of woodland of varying width but often about 80–150 ft. (24–45 m.) and variously oriented are found in situations exposed in different degree. Some have been planted as continuous belts bordering estates or round arable fields, others running north and south protect crops and stock or are planted on the south or west sides of coniferous woods. The predominant constituent of these woodlands is beech, and there is reason to believe that it was so planted, although decaying stumps show that in some woods where beech is now pure, other trees (e.g. silver fir, larch) were at one time growing with it.

The soils upon which they are planted vary in depth and less so in texture, the information on this subject resting mainly on occasional exposed root systems and the surface soil layers. Generally the soils may be described as sands or sandy loams, their composition varying according to the geological formation (Old Red Sandstone, Triassic Elgin Sandstone, Granites, etc.) from which the glacial till has its origin. Some of these soils are ridged, and indicate at least preparation for arable cultivation, although the presence of numerous boulders in some lend colour to the belief that the ground was never actually ploughed.

Most of the trees in these shelterbelts are old, probably 100 years or more and, although the canopy is usually continuous, the trees are not as a rule dense upon the ground. The height of the crowns and the width of the belt exclude light as a factor having a deciding influence on the composition of the vegetation in different parts of the belt. (This is true of course only for those shelterbelts which are open on both flanks.) In fact this shelterbelt vegetation is specialised and may be compared to the vegetation of the exposed margins of some Danish beechwoods (18), but in our case there is no hinterland of extensive beechwood with which comparison may be made and relationships established.



The shelterbelt beechwoods consist only of two strata, the tree layer and the layer of grasses and herbs. The shrub layer exists only in embryo in the scattered and sometimes frequent small rowans and in the locally frequent rowans in gaps. In the subsidiary vegetation the hemicryptophytes preponderate.

There are two distinct types, the *Holcus* type and the *Deschampsia* type, named after the respective dominants, *Holcus mollis* and *Deschampsia flexuosa*. Generally speaking the *Holcus* type occupies the less exposed areas, the *Deschampsia* type the more exposed. The main species of each type with their constancy and average frequency values are listed on pp. 146, 147. These data are obtained from thirty-one examples of the *Holcus* type and twenty-two of the *Deschampsia* type.

The chief obvious factor differentiating these two types is exposure to the wind, but this is modified by the soil quality and tree root competition. Beech leaves when dry curl up at their edges and are readily blown away during the winter months from the low-growing mat of *Deschampsia* whose form is determined partly by the shade and partly by the root competition of the beech trees (for experimental evidence, v. Part II: Tree roots and the subsidiary vegetation). Locally where the wind has not the same free play, *Holcus* and its associates are found, e.g. in hollow stumps, in soil depressions, in cart tracks and between boulders. Where shelter exercises an influence over a greater area, then the *Holcus* type replaces the *Deschampsia*, and this is found as a narrow strip behind dykes on the windward side and, to a greater extent, in the rear of the shelterbelts where some of the litter accumulates. Unlike *Deschampsia*, *Holcus* has a growth form which tends to retain the litter, and this property enables the *Holcus* community to extend at the expense of the *Deschampsia*, for, along the boundary, the removal of the litter reveals the dead remains of *Deschampsia flexuosa*.

Besides originating in this way the *Holcus* type is found generally in the more sheltered places, but within it *Deschampsia* is locally dominant, especially where the ground is slightly raised, e.g. at the foot of trees, and where locally there is greater exposure to the wind. But this type may be found even in relatively exposed places if the soil is fertile.

In addition to the above, and indeed connected with them, is a third factor, root competition. *Holcus* is seldom absent from the *Deschampsia* type, and apart from its occurrence in sheltered places it is an occasional constituent in many of the woodlands. In some of them tufts of well-grown *Holcus* are found on the raised mat of *Deschampsia* which is occasionally found round the bases of beech trees. These tufts are more frequent on the south-west sides. Also in some gaps *Holcus* increases in vigour and frequency, and this is not wholly due to the additional light but to the diminishing severity of tree root competition. Root cutting experiments support this. Further, the addition of litter held in place by wire-netting not only kills out the *Deschampsia* but promotes the



normal growth of *Holcus* even in exposed woods. Apparently therefore the aerial parts of *Holcus* can withstand exposure to the wind provided the substratum supplies the needs of the plant and both the cutting of the tree roots and the addition of litter bring about similar results. (For experimental evidence, v. Part II: Tree roots and the subsidiary vegetation.)

*Comparison of the Holcus and Deschampsia types.*

(1) *Floristic composition.*

*Tree layer.* In the *Holcus* type fourteen tree species are found as compared with nine in the *Deschampsia* type. With the exception of *Quercus sessiliflora* these nine are common to both, and the following are absent from the *Deschampsia* type: *Fraxinus excelsior*, *Castanea vesca*, *Tilia vulgaris*, *Acer platanoides*, *Picea excelsa*, *Prunus avium*. It is impossible to state how far this difference is due to the habitat, directly or indirectly, or merely to differences in the original planting, but *Deschampsia* beechwoods, now pure, show stumps of other species, e.g. *Abies pectinata*, and possibly other conifers. The frequency and constancy of the tree species accompanying beech are nearly always low. After *Fagus* with constancy 5, come *Quercus robur* with 4 in the *Holcus* and 2 in the *Deschampsia* type, and *Acer pseudoplatanus*, with 3 and 2 respectively. The rest have values of 2 or 1.

Measurements and estimates of the height attained by beech yield an average for the *Holcus* type of 75 ft. (23 m.) (average of 24: extremes 62 and 94 ft.): for the *Deschampsia* type 65.5 ft. (20 m.) (average of 27: extremes 41 and 80 ft.). The trees on ridged soil in the *Deschampsia* type are on an average 4 ft. (1.2 m.) taller. Variation is found in the same wood, trees on the windward side being shorter, and having lop-sided crowns. On the whole the beeches in the *Holcus* type are better grown and more free from lichens, but the occurrence of these is very variable even within one wood, and trees with lichens stand side by side with those without. While recorded from all aspects of the stem, lichens are most prevalent on the north and west sides. Associated trees are in general less tall than the beech with the exception of *Abies pectinata*.

In the *Holcus* type beech seedlings are, over all, frequent, in the *Deschampsia* type, occasional, a difference due to factors already discussed (28). This initial advantage is not maintained, for young growth is unable to make headway under the beech canopy and is almost restricted to gaps in both types. Regeneration, however, is far from common, and in the *Deschampsia* type is found in gaps where *Vaccinium myrtillus* dominates. In the *Holcus* type, regeneration may occur under the shade of *Ulmus glabra* and *Fraxinus excelsior*.

*Acer pseudoplatanus* seedlings are occasional to locally frequent in the *Deschampsia* and occasional to frequent in the *Holcus* type. None apparently survive, for no older plants are seen.

In the *Holcus* type seedlings and young growth of *Fraxinus* are frequent, in some woods abundant, and are growing successfully in gaps, particularly on Old Red Sandstone, where suppressed small plants several years old are found under canopy (29). By contrast ash seedlings are recorded only once from the *Deschampsia* type on Boulder Clay derived from metamorphic rocks, and these were wilting and had discoloured root tips. They are however locally frequent on Old Red Sandstone.

Birch (*Betula* spp.) regeneration is strictly local in both, and no young oaks were seen. Seedlings of the following are very rare: *Abies pectinata* (both types) and *Pseudotsuga taxifolia* (*douglasii*) (*Deschampsia* type).

*Shrub layer.* Although the shrub layer is absent, rudiments of it show 8 species common to both types with *Hedera helix*, *Ligustrum vulgare*, *Sambucus nigra*, *Vinca minor*, in addition in the *Holcus* type. *Sorbus aucuparia* is the most frequent but the individuals are small, varying in height from 1 to 6 in. (2.5–15 cm.), and several years old. The actual number of years they can endure suppression has not been determined. In gaps rowan is frequent to abundant. On the whole it is more frequent in the *Deschampsia* type, in which the constancy value is 5 compared with 4 in the *Holcus* type. All the other species have a low frequency and most are of sporadic occurrence. *Saxothamnus* has a constancy of 3 in both types: *Rubus idaeus*, 3 in the *Holcus* type compared with 1 in the *Deschampsia*.

*Ground flora.* In twenty-two examples of the *Holcus* type the subsidiary vegetation is uniform over the whole area (normal sub-type): the remaining nine form the lee sides of beechwoods where, by the retention of leaf litter, the *Holcus* type replaces the *Deschampsia* in the same woodland (induced sub-type). Of these nine, four adjoin conifer woods or the rowan-birch associates. This separation has been made to see how far the vegetation of the induced sub-type resembles or differs from that of the normal.

Comparison shows that the following species have a higher constancy in the induced sub-type: *Anemone nemorosa*, *Lastrea dilatata*, *Oxalis acetosella*, *Tridentalis europaea*, *Deschampsia flexuosa*, *Galium saxatile*, *Rumex acetosa* and *R. acetosella*. Proximity to woodland accounts for the higher constancy of the first four species (*Tridentalis* is not recorded from the normal sub-type). *Deschampsia* and *Galium*, found on slight eminences (stumps, partly buried boulders) where litter does not lie, represent fragments of the *Deschampsia* type. The higher constancy of *Rumex* spp. is unexplained. Frequency differences are significant only in *Lastrea*.

On the other hand *Deschampsia caespitosa*, *Holcus lanatus* and *Ranunculus acris* have higher constancy values in the normal sub-type.

Apart from these two sets of plants, the normal and the induced *Holcus* sub-types much resemble each other, and may for comparison with the *Deschampsia* type be considered as one.

In the *Holcus* type there are eighty-two species: In the *Deschampsia* sixty-

Table III. *Flora of shelterbelt beechwoods.**Species with constancy 3 or more.*

For those species named in one list and not in the other the data of constancy and average frequency of the contrasted type are given in brackets.

<i>Deschampsia</i> type				<i>Holcus</i> type			
No. of examples	...	...	22	No. of examples	...	...	31
Life form*		Constancy	Average frequency†	Life form*		Constancy	Average frequency†
MM <sub>2</sub>		5	5.0	Fagus silvatica		5	5.0
M-N		5	2.3	Quercus robur		4 (2)	2.0 (1.8)
N		3	1.5	Sorbus aucuparia		4	1.9
				Rubus idaeus		3 (1)	2.1 (2.0)
				Acer pseudoplatanus		3 (2)	1.9 (1.8)
				Sarothamnus scoparius		3	1.7
Ch.		5	4.6	Holcus mollis		5	4.6
G.r.-H.c.-Ch.		5	2.4	Agrostis spp.		5	3.4
Ch.		5 (2)	2.3 (2.0)	Poa pratensis		5	3.0
Ch.		5	2.1	Veronica chamaedrys		5 (2)	3.0 (1.6)
H.c.		5	2.0	Viola silvatica (agg.)		5 (2)	2.7 (1.6)
H.c.		5	1.9	Anthoxanthum odoratum		5	2.4
G.r.		4 (1)	2.6 (2.0)	Veronica officinalis		5	2.0
H.c.		4	2.3	Oxalis acetosella		4	3.3
H.c.		4 (2)	2.2 (2.1)	Deschampsia flexuosa		4	2.6
H.c.		4	2.0	Holcus lanatus		4 (2)	2.2 (1.5)
H.r.		4	1.9	Galium saxatile		4	2.1
G.r.		4	1.7	Dactylis glomerata		3 (1)	2.2 (1.5)
H.r.		3 (2)	1.7 (2.3)	Deschampsia caespitosa		3 (1)	2.1 (1.0)
H.s.		3 (1)	1.9 (1.8)	Luzula pilosa		3	2.1
Ch.		3	1.5	L. erecta		3	1.9
Ch.		3 (1)	1.4 (1.0)	Ranunculus acris		3 (1)	1.9 (1.0)

\* The classification of life forms apart from the trees and shrubs is according to Braun-Blanquet (*Pflanzensoziologie*, 1928, pp. 249-56): MM<sub>2</sub> = mesophanerophytes; M = microphanerophytes; N = nanophanerophytes; Ch. = chamaephytes; H.r., H.s., H.c. = hemicrophyta rosulata, scaposa and caespitosa respectively; G.r. = geophyta rhizomata; T. = therophyta.

† The average frequency has been calculated by assigning numerical values to the frequency symbols according to the scale used by Tansley and Adamson (this JOURNAL, 1926, p. 24); "1," however, has been taken as 1.

Table III (cont.)

<i>Deschampsia</i> type			<i>Holcus</i> type		
	Constancy	Average frequency		Constancy	Average frequency
<i>Minium hornum</i>	5	3.0	<i>Minium hornum</i>	5	2.5
<i>Hypnum cupressiforme</i>	5	2.8	<i>Hypnum cupressiforme</i>	5	2.0
<i>Dicranum scoparium</i>	5	2.7	<i>Hylocomium triquetrum</i>	4	2.7
<i>Polytrichum commune</i> and <i>formosum</i>	4	3.1	<i>Polytrichum commune</i> and <i>formosum</i>	4	2.4
<i>Hylocomium splendens</i>	4 (2)	3.0 (2.0)	<i>Eurhynchium praelongum</i>	4 (1)	1.9 (1.0)
<i>H. triquetrum</i>	4	2.8	<i>Plagiothecium undulatum</i>	3	2.0
<i>Plagiothecium undulatum</i>	4	2.5	<i>Eurhynchium myurum</i>	3 (2)	1.8 (2.3)
<i>Hypnum schreberi</i>	3 (1)	2.4 (2.0)	<i>Catharina undulata</i>	3 (0)	1.8 (0)
<i>Brachythecium purum</i>	3	2.1	<i>Brachythecium purum</i>	3	1.7
			<i>Dicranum scoparium</i>	3	1.7

*Herbs and grasses of low constancy (2 and 1) exclusive to each type, arranged in life form sub-classes.*

Species exclusive to the *Deschampsia* type

Ch.	<i>Erica cinerea</i>
"	<i>Lycopodium clavatum</i>
H.r.	<i>Hieracium pilosella</i>
H.s.	<i>Centaurea nigra</i>

H.s.	<i>Galium verum</i>
H.c.	<i>Nardus stricta</i>
T.	<i>Euphrasia officinalis</i>
"	<i>Stellaria media</i>

Species exclusive to the *Holcus* type

Ch.	<i>Sagina procumbens</i>
H.r.	<i>Primula vulgaris</i>
"	<i>Plantago lanceolata</i>
H.s.	<i>Achillea millefolium</i>
"	<i>Aegopodium podagraria</i>
"	<i>Angelica silvestris</i>
"	<i>Cirsium lanceolatum</i>
"	<i>C. palustre</i>
"	<i>Epilobium montanum</i>
"	<i>Geum urbanum</i>

H.s.	<i>Heracleum sphondylium</i>
"	<i>Prunella vulgaris</i>
"	<i>Scrophularia nodosa</i>
"	<i>Stachys silvatica</i>
"	<i>Urtica dioica</i>
"	<i>Valeriana officinalis</i>
"	<i>Vicia sepium</i>
H.c.	<i>Alopecurus pratensis</i>
"	<i>Arrhenatherum elatius</i>

H.c.	<i>Cynosurus cristatus</i>
"	<i>Juncus effusus</i>
"	<i>Poa trivialis</i>
G.r.	<i>Agropyrum repens</i>
"	<i>Equisetum arvense</i>
T.	<i>Crepis virens</i>
"	<i>Galium aparine</i>
"	<i>Geranium robertianum</i>
"	<i>Lapsana communis</i>

two. Fifty-four are common to both, while twenty-eight are confined to the *Holcus* and eight to the *Deschampsia* type. Of the twenty-eight only five have a constancy of 2: the rest have 1. Of the eight, one has a constancy of 2, the remainder being of constancy 1.

The bulk of the species are, therefore, the same in both, and differences in the frequency and constancy values account for the different physiognomies. The distribution of these fifty-four species in constancy classes in the two types is set out below.

Constancy ... ..	5	4	3	2	1
<i>Deschampsia</i> type ... ..	6	6	4	10	28
<i>Holcus</i> type ... ..	7	4	5	15	23

There are only sixteen, therefore, in each type with constancy 3 or more (see list p. 146). Ten species are common to both lists. Of these *Deschampsia* and *Poa pratensis* differ significantly both in constancy and frequency: *Agrostis* spp., *Holcus mollis* and *Oxalis* in frequency only: *Anthoxanthum*, *Galium*, *Luzula erecta*, *L. pilosa* and *Veronica officinalis* in constancy only. And it is those which differ in frequency that confer distinctive appearances on the two types.

The following six species have constancy 3 or more in the *Deschampsia* type, but less than 3 in the *Holcus*: *Vaccinium myrtillus*, *Festuca ovina*, *Trisetalia europaea*, *Calluna vulgaris*, *Lastrea dilatata* and *Potentilla erecta*.

The following six have constancy 3 or more in the *Holcus* type but less than 3 in the *Deschampsia*: *Viola silvatica* (agg.), *Veronica chamaedrys*, *Holcus lanatus*, *Deschampsia caespitosa*, *Dactylis glomerata* and *Ranunculus acris*.

The first set of six contains those species which are common in the heath woods described in Part II; the second may be characterised as indicative of an environment less hostile to plant life generally.

In addition to the foregoing data relative to constancy and frequency the following notes on the vigour and general behaviour of certain species are given.

*Deschampsia flexuosa*. In the *Deschampsia* type this plant forms a low continuous mat, its thickness varying with the density of the beech. Where beech is very dense *Deschampsia* is patchy and the soil is partly occupied by lichens. Where the beech is much less dense the thicker mat of *Deschampsia* may be invaded by *Holcus mollis*. Flowering is generally sparse, but vegetative vigour and flowering are much increased by cutting the tree roots.

In the *Holcus* type, *Deschampsia* is distinctly local, being found generally in places more exposed than the normal, and occasionally where the tree stems are denser.

*Holcus mollis*. In the *Deschampsia* type, *Holcus* is generally an occasional, non-flowering, undersized plant. Its frequency and vigour are higher in favourable places, such as cart tracks, soil depressions, among boulders, in decaying stumps, in the neighbourhood of rabbit burrows, upturned roots, in gaps, among 8 in. (20 cm.) tall *Vaccinium myrtillus*, on heaps of dumped soil, and occasionally at the foot of beech trees. Generally speaking *Agrostis* spp. accompany *Holcus* in places rendered suitable by the presence of leaf litter.

*Oxalis acetosella*. While generally distributed as an occasional plant in the *Deschampsia* type, *Oxalis* usually remains a small non-flowering plant with leaves from 6 to 9 mm. across. In the *Holcus* type and its representative fragments in the *Deschampsia* type, *Oxalis* grows much more vigorously with leaves often 1 in. (2.5 cm.) across. *Anemone nemorosa* behaves in the same way as *Oxalis*.

*Vaccinium myrtillus*. As a small plant with a semi-procumbent stem about 3 in. (7.5 cm.) long, *Vaccinium* is generally distributed in the *Deschampsia* type. Along wood margins and in gaps it grows much more vigorously, and may become locally dominant attaining a height up to 14 in. (35 cm.). Under shade the vigour of the small plants is unaffected by cutting the tree roots.

In the *Holcus* type its occurrence is local; it is generally found where *Deschampsia* occurs.

*Mosses*. All the eighteen species recorded from the *Deschampsia* type are found in the *Holcus* type, which includes the following additional three: *Catharinea undulata*, *Eurhynchium piliferum* and *E. striatum*.

For those with constancy 3 or more see the list of species, p. 147. Seven species are common to both lists: in the *Deschampsia* type *Hylocomium splendens* and *Hypnum schreberi* are additional, and in the *Holcus* type *Eurhynchium praelongum*, *E. myurum* and *Catharinea undulata*.

The resemblance to the conifer heath woods of Part II is again emphasised in the distinctly higher constancy and average frequency of *Hylocomium splendens* and *Dicranum scoparium*, and in the higher constancy of *Hypnum schreberi*. *Eurhynchium praelongum* has a higher constancy in the *Holcus* type, whilst *Catharinea undulata* is limited to it.

All the species of vascular plants and mosses are found in several plant communities and probably none has a higher exclusiveness value than 2.

## (2) Life form.

The percentage distribution of the life forms of the ground vegetation of the two types is given below. The numbers in brackets are the actual numbers of species.

Table IV.

		Ch.	H.r.	H.s.	H.c.	G.r.	G.b.	G.rad.	T.	Total
All species	<i>Deschampsia</i> type	20.5 (13)	17.5 (11)	24 (15)	22 (14)	8 (5)	1.5 (1)	1.5 (1)	5 (3)	100 (63)
			63.5 (40)			11 (7)				
	<i>Holcus</i> type	14.5 (12)	14.5 (12)	32.5 (27)	22 (18)	8.5 (7)	1 (1)	1 (1)	6 (5)	100 (83)
			69.0 (57)			10.5 (9)				
Species with constancy 3 or more	<i>Deschampsia</i> type	6	2	1	6	3	—	—	—	18
	<i>Holcus</i> type	5	2	1	8	2	—	—	—	18
Species found in one type only	<i>Deschampsia</i> type	2	1	2	1	0	—	—	2	8
	<i>Holcus</i> type	1	2	14	5	2	—	—	4	28



The significant feature in the first two sets of spectra is the high percentage of chamaephytes, which may be interpreted as due to the proximity of the sea and as an expression of the relatively mild winter conditions experienced in the lowlands of the north-east of Scotland (p. 140). In this connection reference may be made to *Rubus fruticosus* (agg.) which is given by Raunkiaer as a hemicryptophyte in Denmark, but which in the lowlands of eastern Scotland is chamaephytic or phanerophytic. Inland, at higher altitudes on Deeside, *Rubus* is not found, for example, at Balmoral (alt. 950 ft.—290 m.); and the local residents on Deeside state that it disappears above a certain altitude (undetermined). This sensitive behaviour of *Rubus* and other plants (for example *Holcus mollis*, which is often chamaephytic), responding as they do to the winter conditions of a varied topography, suggests a profitable field for the comparison of local climates within a given area and for the purposes of the study of natural vegetation may connote more than plant zones delimited by the cultivation of agricultural crops.

In the spectrum of species with constancy 3 or more ten species are common to both types and the slight differences in numbers are due to the distribution of the remaining six in the life-form sub-classes. In the *Deschampsia* type the chamaephytes *Vaccinium* and *Calluna* replace *Veronica chamaedrys* in the *Holcus* type: the rosette hemicryptophyte *Lastrea* (with however a slightly higher average frequency in the *Holcus* type) replaces *Viola silvatica* (agg.); *Potentilla*, with leafy flowering stems, replaces *Ranunculus*: the caespitose *Festuca* replaces *Holcus lanatus*, *Dactylis* and *Deschampsia caespitosa*, while the rhizome geophyte *Trientalis* is additional in the *Deschampsia* type.

Taking all three sets of spectra into account, there is a slight but consistently higher number of chamaephytes in the *Deschampsia* type, and a consistently higher number of caespitose hemicryptophytes in the *Holcus* type. The chief difference, however, lies in the pre-eminence of the hemicryptophyta scaposa in the *Holcus* type—seen in the spectrum of “all species” and particularly in the spectrum of those found in one type only.

These hemicryptophyta scaposa are nearly all tall growing herbs adapted to more mesophytic conditions and it is concluded that exposure to wind in the *Deschampsia* type is definitely prejudicial to the occurrence of this life form. A comparison of the other species supports this conclusion: those of the *Holcus* type are more mesophilous than those of the *Deschampsia* type.

On the other hand significant species (with constancy 3 or more), the average height of whose leaves is nearer the ground level, tend to be excluded and to show a reduced constancy and/or average frequency in the *Holcus* type as compared with the *Deschampsia* type; for example, *Deschampsia flexuosa*, *Vaccinium*, *Galium saxatile*, *Luzula erecta*, *L. pilosa*, *Festuca*, *Potentilla* and *Calluna*.

From this analysis and from the observations respecting the behaviour of some species in both types (p. 148) the general conclusion is reached that the habitat (including beech root competition) of the *Deschampsia* type is limiting to, or less than optimal for, the species characteristic of the *Holcus* type, but that competition excludes or tends to exclude species characteristic of the *Deschampsia* type. In this competition beech leaf litter plays an important part<sup>1</sup>.

(3) *Structure and life history.*

In the *Deschampsia* type the number of trees per 10,000 square feet (= 0.23 acre = 0.093 hectare) of five woodlands, together with the height of a beech of average diameter in each, are given in the following table. All the woodlands are growing on ridged soil except No. 2.

Table V.

	1	2	3	4	5
<i>Fagus</i> dominant ... ..	16	14	29	15	20
sub-dominant ... ..	4	3	4	2	2
" <i>pseudoplatanus</i> sub-dominant	1	—	—	—	—
<i>Larix decidua</i> dominant ... ..	—	—	3	—	—
Totals ... ..	21	17	36	17	22
Average girth in feet and inches of dominant <i>Fagus</i> ... ..	5 5½	5 0	3 5	4 11	4 7
Height of dominant <i>Fagus</i> in feet	77	70.5	66	63	67

No data of a similar kind have been obtained for the *Holcus* type. In neither type is there a shrub layer with normal tree density, but along wood margins and under a more open canopy (e.g. with 6 stems per 10,000 square feet) *Deschampsia flexuosa* is succeeded in dominance by *Vaccinium myrtillus*. Here trees may establish themselves freely and, in the absence of grazing, rowan may form thickets in which are found occasional birch and beech. Sometimes young beech is locally dominant.

The later stages of the life history of the *Deschampsia* shelterbelts seem therefore clear, but since these adult shelterbelts are essentially similar to the adult beechwoods described in Part II (The adult beechwood), further description is not given here, but we may remark that the retention of beech leaves by the *Vaccinium* stems promotes the increase of *Holcus mollis* and *Oxalis acetosella*, whilst the improved illumination favours *Calluna vulgaris*.

In gaps in the *Holcus* type, birch is on the whole more frequent than rowan and after felling birch may colonise the ground freely. What happens to the ground vegetation with opening up of the wood is not determined in all cases with certainty, but in some examples *Holcus* is followed by *Vaccinium* (Part II: The adult beechwood).

<sup>1</sup> The same phenomenon will be more fully analysed in a paper on the vegetation of the Chiltern Hills to appear in a future issue of this JOURNAL.

An interesting example of beech regeneration is found in the background of a *Deschampsia* shelterbelt (Fig. 1). The young beeches are from 8 to 20 ft. (2.4 to 6 m.) high, and some are supported by stilt roots arising from a soil covered by a layer of laminated beech leaves 1 to 3 in. (2.5 to 7.5 cm.) thick, and so closely matted that the surface is slippery and springy under foot. The present surface is altogether unsuitable for beech regeneration and is occupied by an open community of the plants given below, much of the surface being,

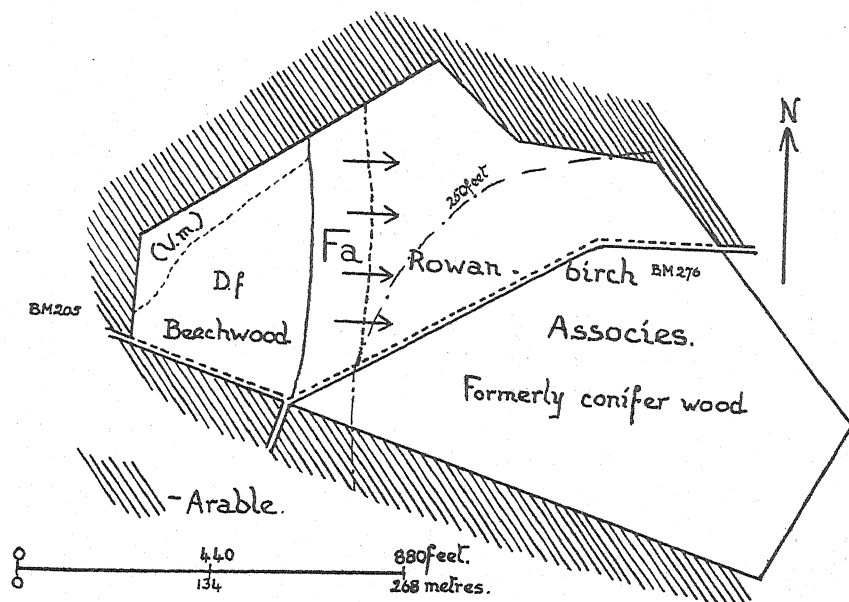


FIG. 1. *Grandholme*. Planted beechwood on ridged soil occupies the western part. Along the north-west margin of the beechwood *Vaccinium myrtillus* (V.m.) is dominant; elsewhere *Deschampsia flexuosa* (D.f.). The rest of the area bears a rowan-birch associates occupying the site of a felled conifer wood. Where beech adjoins the rowan-birch associates invasion gives rise to the beech associates (Fa). The arrows show the general direction of beech invasion.

however, bare, and colonisation by vascular plants taking place very slowly. Dead stocks of *Lastrea dilatata* and larch stumps also occur.

<i>Sorbus aucuparia</i> (small)	o.—f.	<i>Luzula pilosa</i>	l.f.
<i>Deschampsia flexuosa</i>	o.—f.	<i>Trientalis europaea</i>	o.—l.f.
<i>Galium saxatile</i>	o.	<i>Vaccinium myrtillus</i> (small)	o.
<i>Holcus mollis</i>	l.		
<i>Dicranella heteromalla</i>	f.—l.d.	<i>Mnium hornum</i>	o.—l.d.
<i>Dicranum scoparium</i>	o.	<i>Lophocolea bidentata</i>	f.
<i>Hypnum cupressiforme</i>	o.	Lichens	l.a.

The removal of the layer of beech leaves uncovers dead rhizomes of *Holcus mollis* in the hollows and of *Holcus* rhizomes and *Deschampsia flexuosa* leaves on the ridges, overlying a black peaty layer 0.75 in. (19 mm.) thick. This in turn rests on the mineral soil. The history of the area may be reconstructed as follows. An area more sheltered formerly than now allowed the beech

litter to accumulate, overwhelming the *Deschampsia* and allowing the *Holcus* to extend from the hollows on to the ridges. Before or after the removal of the conifers, and in any case before *Vaccinium myrtillus* invaded and became dominant, rowan and beech regeneration took place and suppressed all other plants. The wind then had free play, and the accumulated litter, decomposing slowly, settled down and formed a mat, leaving the tree roots exposed. The young beeches now look unhealthy.

Another instructive example occurs nearby, where the locally dominant beech, from 30 to 40 ft. (9 to 12 m.) high, has colonised and then suppressed dominant *Vaccinium myrtillus*, whose remains are found in the humus now colonised and dominated by *Mnium hornum*.

#### (4) *Habitat*.

The main habitat difference separating the *Deschampsia* from the *Holcus* type is exposure to the wind, which may act directly, presumably with greater effect on the trees, but its chief effect on the ground flora would appear to be due to the removal of the beech leaf litter.

In the *Deschampsia* type the more xerophilous plants dominate, and *Deschampsia flexuosa* forms a black often powdery friable humus with an average depth of 2 to 3 in. (5 to 7.5 cm.) (extremes 0.5 to 8 in.). The mineral soil underlying this may or may not show definite bleaching or contain much infiltrated humus. On ridged soils no visible bleaching of the upper soil layers is found, but under the laminated beech litter mentioned above (p. 152) bleaching becomes apparent. The following data offer a comparison between the profiles of the ridged soil with and without accumulated litter.

Table VI.  
Without litter

	pH	Zone
	3.6	1. 1.3 cm. <i>Deschampsia</i> friable humus
Uppermost 10 cm.	4.0	2. 35 cm. Dark sandy soil. Uniform colour throughout
Next 10 cm.	4.3	
Lowest 12.5 cm.	4.3	
	4.6	3. Soft humus-iron pan. Roots of trees and other plants penetrate
	4.75	4. 29-30 cm. reddish sandy loam
		5. At 70 cm. grey fairly compact soil
With litter		
	3.8	1a. 3.8 cm. laminated beech leaves with dead <i>Holcus</i> rhizomes
	3.8	1b. 1.9 cm. black peaty layer ( <i>Deschampsia</i> ?)
		2a. About 0.6 cm. distinctly bleached layer
		2b. About 0.6 cm. containing much humus (peat)
Uppermost 10 cm.	4.0	2c. 27.5 cm. dark sandy soil. Upper zone distinctly paler than lower but no sharp line of demarcation
Next 10 cm.	4.0	
Lowest 7.5 cm.	4.1	
		3. Iron pan
	4.6	4. 25 cm. reddish sandy loam
	4.75	5. At 60 cm. grey fairly compact soil

The existence of a distinct bleached zone and the lower pH values in zone 2c of the profile "with litter," than in zone 2 of the profile without, suggest a hostile influence of the compacted beech leaf litter.

Earthworms have been seen but they are very rare. When, however, beech litter is laid down and held in place, earthworms, which may have been brought in with the litter, laid down experimentally, do survive.

In many of the *Holcus* types the soil is more sandy or of greater fertility. There is no accumulation of raw humus and no sharp line of demarcation exists between the mould and the mineral soil. No distinct bleached layer was observed. Earthworms are frequent, both in the "normal" and in the "induced" *Holcus* sub-types, and perhaps shelter from drying winds enables these animals to survive here.

## HERBACEOUS BEECHWOODS.

The short account of herbaceous beechwoods given here is merely a recognition of their existence. Only six have been examined (list of species, pp. 154-5). The small number is partly accounted for by the fact that few exist compared with the number of grassy shelterbelts and that in the situations bearing a vegetation of this kind other broad-leaved trees have commonly been planted either with or without beech.

Table VII. *Herbaceous beechwoods.*

List of herbs and mosses occurring in three or more of the examples and/or with an average frequency of 2.0 or over.

Life form	Reference No. ...	1	2	3	4	5	6	Average frequency
H.s.	<i>Stellaria nemorum</i>	—	—	—	—	d.	—	5.0
H.r.	<i>Sanicula europaea</i>	—	—	—	a.—d.	—	—	4.5
H.c.	<i>Luzula maxima</i>	a.	d.	o.—l.f.—l.d.	—	l.a.	m.l.d.	3.8
G.r.	<i>Anemone nemorosa</i>	—	a.—l.d.	r.—l.a.	o.	a.—l.d.	d.	3.4
H.s.	<i>Ranunculus ficaria</i>	—	—	—	—	l.a.	—	3.0
G.r.—H.c.—Ch.	<i>Holcus mollis</i>	l.a.	o.	—	l.f.—l.d.	l.a.—l.c.d.	—	2.9
H.s.	<i>Ajuga reptans</i>	—	—	—	l.a.	—	o.—l.a.	2.8
H.r.	<i>Oxalis acetosella</i>	l.	a.—l.d.	o.	l.f.	a.—l.d.	o.—l.a.	2.6
T.	<i>Geranium robertianum</i>	—	o.	—	o.	f.	—	2.3
H.r.	<i>Lastrea dilatata</i>	—	f.—l.a.	o.—l.f.	—	o.	o.	2.3
H.r.	<i>Primula vulgaris</i>	—	l.f.	—	o.—l.a.	—	o.—l.a.	2.3
H.s.	<i>Ranunculus repens</i>	—	l.	—	+	l.f.	l.d.	2.3
H.r.	<i>Dryopteris filix-mas</i>	o.	o.	o.—l.a.	+	o.	o.—l.a.	2.2
H.s.	<i>Lychnis dioica</i>	—	o.	—	o.	l.f.—l.a.	—	2.2
H.r.	<i>Viola silvatica</i> (agg.)	o.	o.—l.a.	—	o.—l.f.	o.	—	2.1
H.s.	<i>Adoxa moschatellina</i>	—	—	—	l.	f.	—	2.0
T.	<i>Arenaria trinervia</i>	o.—l.f.	—	—	o.—l.f.	—	—	2.0
G.r.	<i>Asperula odorata</i>	—	—	—	l.f.	—	—	2.0
H.c.	<i>Festuca gigantea</i>	—	—	—	o.	—	—	2.0
Ch.	<i>Galium saxatile</i>	—	—	o.	—	—	o.	2.0
H.s.	<i>Heracleum sphondylium</i>	—	—	—	—	m.l.f.	—	2.0
H.s.	<i>Hieracium vulgatum</i>	o.	—	—	—	l.f.	—	2.0
T.	<i>Lapsana communis</i>	o.	—	—	—	o.	—	2.0
H.c.	<i>Luzula pilosa</i>	—	—	—	—	—	l.f.	2.0
Ch.	<i>Lysimachia nemorum</i>	—	—	—	o.	—	o.—l.f.	2.0
H.s.	<i>Mercurialis perennis</i>	—	l.f.	—	—	l.f.	—	2.0
G.r.	<i>Poa pratensis</i>	o.	—	—	—	o.	—	2.0
H.r.	<i>Polypodium vulgare</i>	—	—	o.	—	—	—	2.0
G.r.	<i>Pteridium aquilinum</i>	—	o.	—	—	—	—	2.0
H.s.	<i>Rumex acetosa</i>	—	—	—	—	l.f.	—	2.0
H.s.	<i>Senecio</i> sp.	o.—l.f.	—	—	o.	—	—	2.0
Ch.	<i>Stellaria holostea</i>	—	—	—	—	l.f.	—	2.0
H.r.	<i>Taraxacum officinale</i>	o.	—	—	—	—	—	2.0

Table VII (cont.)

Life form	Reference No. ...	1	2	3	4	5	6	Average frequency
Ch.	<i>Veronica chamaedrys</i>	o.	o.—l.f.	l.	l.f.	o.—l.f.	f.	2.0
Ch.	<i>V. montana</i>	—	r.—o.	—	l.	l.f.	f.—a.	2.0
H.s.	<i>V. serpyllifolia</i>	—	—	o.	—	—	o.	2.0
H.s.	<i>Vicia sepium</i>	—	—	—	o.	—	—	2.0
H.c.	<i>Agrostis vulgaris</i>	o.	o.	l.	o.	o.—l.f.	o.—l.f.	1.9
T.	<i>Galium aparine</i>	r.	l.	—	—	f.	o.	1.8
H.s.	<i>Geum urbanum</i>	—	—	—	l.	o.—f.	o.	1.8
Ch.	<i>Veronica officinalis</i>	o.	l.	o.—l.f.	—	—	o.—l.f.	1.8
H.r.	<i>Blechnum spicant</i>	—	o.—f.	o.l.	—	—	l.f.	1.7
G.b.	<i>Conopodium majus</i>	—	o.	—	o.	r.	—	1.7
H.c.	<i>Dactylis glomerata</i>	—	r.—o.	—	o.—l.	o.	—	1.7
H.c.	<i>Holcus lanatus</i>	l.f.	r.	—	—	l.f.	l.f.	1.7
H.s.	<i>Urtica dioica</i>	—	—	l.	l.f.	o.	—	1.7
H.c.	<i>Deschampsia caespitosa</i>	r.	r.—o.	—	—	o.	—	1.5
H.s.	<i>Digitalis purpurea</i>	o.	r.	—	—	—	l.	1.3
H.c.	<i>Festuca rubra</i>	o.	l.	—	—	l.	—	1.3
H.s.	<i>Prunella vulgaris</i>	r.	l.	l.	o.	—	—	1.3
	<i>Mnium hornum</i>	o.—l.d.	d.	l.d.	l.a.	o.—l.d.	o.	3.3
	<i>Hylocomium loreum</i>	—	—	l.f.	—	—	l.a.	2.5
	<i>Thuidium tamariscinum</i>	—	—	l.	—	—	a.	2.5
	<i>Hypnum cupressiforme</i>	l.d.	o.	o.	l.d.	l.	o.	2.5
	<i>Eurhynchium striatum</i>	l.f.	—	o.	—	—	l.a.	2.3
	<i>Hylocomium triquetrum</i>	—	—	l.f.	—	—	o.—l.a.	2.3
	<i>Plagiothecium undulatum</i>	o.	l.a.	o.	—	—	o.	2.3
	<i>Polytrichum formosum</i>	—	l.a.	o.—l.f.	—	l.f.	o.	2.3
	<i>Brachythecium rutabulum</i>	—	—	—	l.f.	o.	o.	2.0
	<i>Dicranum scoparium</i>	—	—	o.	—	—	o.	2.0
	<i>Eurhynchium myurum</i>	o.	—	o.	o.	—	o.	2.0
	<i>Mnium undulatum</i>	—	—	o.	o.	l.f.	o.—l.f.	2.0
	<i>Catharina undulata</i>	—	l.	o.	l.f.	—	o.	1.8
	<i>Eurhynchium praelongum</i>	l.f.	l.	o.l.	l.a.	o.	o.	1.8

The beech has a smooth, white bark, with or without lichens, and attains a large size, the average height of trees measured from three of the woods being 92 ft. (28 m.) (extremes 86 and 100). Young beech is recorded from five of the woods.

There is no shrub layer.

A sufficient number of woods has not been examined for a detailed analysis of the ground flora, but herbs, with *Luzula maxima*, predominate. *Luzula maxima* is found in all except No. 4, where *Sanicula europaea* is dominant. The soil of this wood has a pH of 6.0. *Luzula maxima* is dominant in No. 2, and will probably dominate when woods 1 and 3 open out with age. In No. 5 *Stellaria nemorum* dominates, but under deeper shade it becomes a smaller and less frequent plant, and *Anemone nemorosa*, *Oxalis acetosella* and *Scilla non-scripta* become more conspicuous. In wetter parts *Stellaria* forms a seasonally complementary society with *Ranunculus ficaria*. In No. 6 *Anemone nemorosa* is dominant and the spring facies of *Anemone* is followed later in the damper parts by one of *Ranunculus repens*.

The species of the ground vegetation yield the following spectrum:

Ch.	H.r.	H.s.	H.c.	G.r.	G.b.	T.	Total
16 (11)	13 (9)	37 (25)	15 (10)	9 (6)	4 (3)	6 (4)	100 (68)
	65 (44)			13 (9)			



The hemicryptophytes, with 65 per cent., predominate, but the "oceanic" influence is revealed in the high percentage of chamaephytes.

Compared with the spectra of the *Deschampsia* and *Holcus* types the spectrum of the herbaceous woods shows a higher percentage of hemicryptophyta scaposa and a lower percentage of hemicryptophyta caespitosa. The presence of *Allium ursinum* and *Scilla non-scripta* is responsible for the higher percentage of geophyta bulbosa. This maximum of species with leafy flowering stems emphasises the favourable moisture conditions of the habitat of the herbaceous type<sup>1</sup>.

All six woods are found on Old Red Sandstone, and in sheltered places or where the air is humid. Nos. 1 and 4 occupy slopes facing the Beaulieu and Cromarty Firths: Nos. 2, 3 and 6 occur on steep slopes of valleys cut in the soft rock, while No. 5 occurs in the bottom of a valley.

The soil in all cases is deep and distinctly loamy, Nos. 5 and 6 being heavier. Earthworms are abundant and there is no accumulation of beech leaves on the surface, but there is a good mould. Below, there is no visible bleaching, but in No. 6, which is irregularly ridged by flushes arising high up the slope, the crests of the ridges show a distinct bleached layer, 3 in. (7.5 cm.) thick, under .5 in. (1.3 cm.) of black humus and 3.5 in. (8.8 cm.) of mineral soil coloured black by infiltrated humus.

#### THE RELATIONSHIP OF THE HERBACEOUS AND GRASSY BEECHWOODS TO OTHER PLANT COMMUNITIES.

It is premature to give a considered judgment on the exact affinities of the woodlands described, but certain broad statements are admissible. The herbaceous beechwoods are found on soils which, although fertile, have on account of their situation never been cultivated. Uncultivated soils of this kind are rare in the north-east of Scotland, and their discontinuous distribution in a countryside occupied by quite different plant communities puts a serious check upon the free migration of plants from one area to another. It is probable, therefore, that some of these slopes have been continuously occupied by subsidiary woodland plants whether the woody vegetation itself has been continuous or not. To this extent the vegetation may be considered natural, and affords a clue to its relationship with other plant communities. In No. 6 further evidence is afforded by the oakwood which continues the beechwood along the slope. The following woody plants with their frequencies are found in this oakwood:

<i>Quercus robur</i>	f.—a.	<i>Populus tremula</i>	l.a.
<i>Fraxinus excelsior</i>	o.—l.d.	<i>Prunus spinosa</i>	o.—l.d.
<i>Fagus sylvatica</i>	o.	<i>P. padus</i>	r.
<i>Prunus avium</i>	o.	<i>Corylus avellana</i>	l.
<i>Betula pubescens</i>	o.	<i>Crataegus</i> sp.	+
<i>Alnus glutinosa</i>	l.	<i>Salix caprea</i>	+
<i>Sorbus aucuparia</i>	f.—l.a.	<i>Lonicera periclymenum</i>	l.a.

<sup>1</sup> The spectrum should be compared with that for the beechwoods of chalk escarpments in Southern England which will be given in a paper on the vegetation of the Chiltern Hills in a future issue of this JOURNAL. The spectrum of the herbaceous type differs chiefly in the higher percentage of chamaephytes and the lower percentage of geophytes.

In the other woods the evidence is not so satisfactory, but on the whole there is affinity with the damp oakwood of lighter loams.

In the grassy beechwoods there is nothing very distinctive, the subsidiary vegetation being composed of the elements of neighbouring plant communities (natural and artificial) which can survive the new conditions introduced by the planting of beech. Some undescribed beech woodlands from Perthshire show unmistakable relationship with the dry oakwood, one indeed adjoining such an oakwood with *Holcus mollis* (d.), *Pteridium aquilinum* (a.-d.), *Teucrium scorodonia* (f.), *Scilla non-scripta* (o.). Again one of the examples of the *Holcus* type adjoins a woodland of oak-birch with *Lastrea dilatata* and *Holcus mollis* the most conspicuous plants, and it is probable that several examples of the *Holcus* type have similar affinities. On the other hand some examples of the *Deschampsia* and of the "induced" *Holcus* types are clearly related to the heath woods described in Part II.

(To be continued.)

## THE BOREAL HAZEL FORESTS AND THE THEORY OF POLLEN STATISTICS

By G. ERDTMAN.

(*With two Figures in the Text.*)

IN the summers of 1922-7 I had the pleasure of travelling in the British Isles in connection with some investigations of the Late Quaternary history of the forests. As a summary of my results and some comparisons with forest history on the Continent have recently been published (this JOURN. 17, 1929) I shall here confine myself to a problem bearing on the theory of pollen statistics, to the solution of which a continued study of the history of British vegetation ought to furnish important data. To some extent this problem is connected with the much debated question of the "boreal hazel forests." In dealing with those forests Dr Woodhead (*Empire Forestry Journal*, 1928) suggested that the records of hazel as shown in pollen statistics need careful scrutiny, and there are certainly many who would agree with him on that point. Prof. von Post was the first to argue, on the basis of pollen statistics, that the hazel in certain places once formed real forests. He further suggested that the boreal hazel forests of south Sweden represented a somewhat maritime forest type. Others, e.g. Rudolph and Stark, held the hazel forests to be rather of a continental type, indicating conditions somewhat similar to those found at the present day in the forest steppe zone of South Russia. With Bertsch I have laid stress on the importance of the ecology of the hazel, especially its great plasticity, for the comprehension of the boreal hazel forests. Thus the hazel forests often covered tracts on the limit of conditions favourable to tree-growth, as along the margins of the boreal steppes and near the sub-alpine region, forming there a more or less pure pioneer scrub before the development of the forest proper.

The hazel forests seem to have been especially characteristic of central and western Europe (Fig. 1). This is worthy of notice, as in our day the hazel is certainly a more prominent element, e.g. in Poland (Volhynia, Podolia, etc.), and parts of Russia than, for instance, in the west of Germany and the British Isles.

The map also indicates the periods at which the hazel was at its maximum. In central and western Europe this occurred, as a rule, during boreal time. The British Isles differ in this respect in that the maximum hazel pollen frequency has been registered in places in post-boreal layers, from atlantic down to sub-atlantic.

No boreal hazel forests have yet been found in the phytogeographically interesting zone<sup>1</sup> stretching from the Baltic to the Black Sea roughly along the Vistula-Dniestr line. East of that zone the hazel pollen maximum is atlantic or sub-boreal.

These differences in the geographical and chronological appearance of the hazel forests still remain to be explained. I shall here only call attention to a matter which in certain cases may have an important bearing on the theory of pollen statistics and which may be considered when trying to explain the presumed "hazel forests."

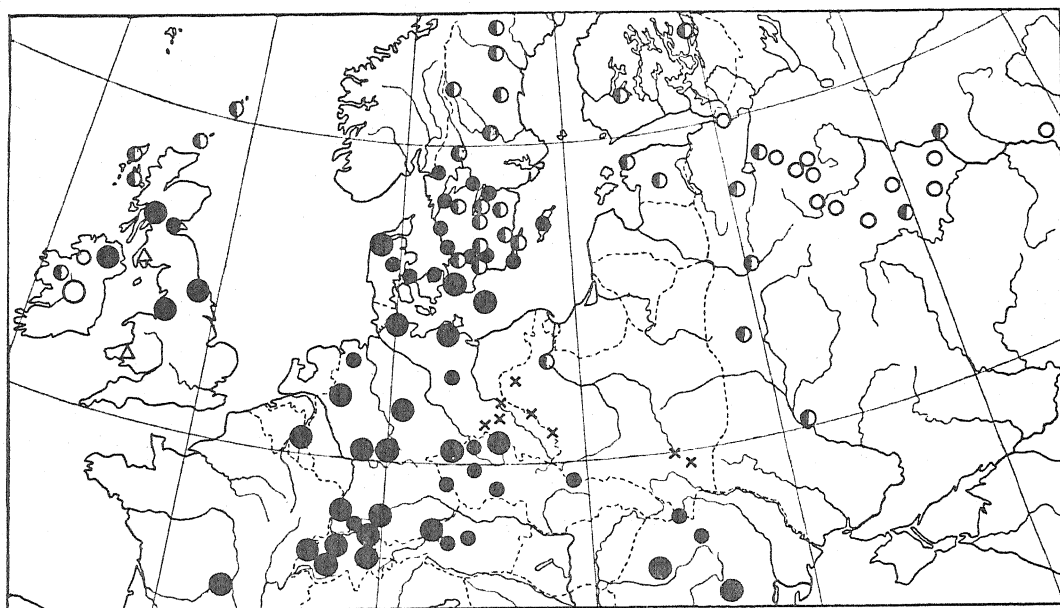


FIG. 1. Map indicating the periods at which the hazel was at its maximum according to pollen statistics.

- Maximum in the boreal period (pollen frequency <100 per cent.)
- " " " " ( " " > " " )
- ⊖ " " atlantic period ( " " < " " )
- " " sub-boreal period ( " " < " " )
- " " " " ( " " > " " )
- △ " " sub-atlantic period
- × No distinct maximum: pollen frequency low.

In dealing with pollen statistics it is impossible to draw any safe conclusions from the pollen content or lack of pollen in a peat or sediment unless we know its approximate capacity to catch and preserve the pollen grains.

<sup>1</sup> In our days characterised among other things by the eastern limit of *Fagus sylvatica* and *Quercus sessiliflora* and the limit between the East-European and the West-European distribution of *Picea excelsa*.

Most of the pollen grains reaching the surface of a bog will not be preserved in a fossil state. The great supply of oxygen, the repeated wetting and drying, etc., which affect the pollen grains will hasten their destruction. The fossil pollen of the bogs, therefore, consists of those grains which were quickly carried down from the bog surfaces on which they landed to deeper levels with a smaller supply of oxygen and better conditions of preservation. Dead bogs, i.e. those where peat is no longer formed, cannot catch and preserve the pollen grains. This will also be the case with living bogs, during their inactive periods, when the cold of the winter, exceptional drought or, in some types of peat deposits, excessive rain puts a temporary stop to the activity of the peat-forming organisms. Owing to its early flowering time (at Coimbra in the North of Portugal even before the New Year, usually about December 27th, at Aberystwyth in Wales January 13th, in Bremen February 23rd, at Karlskrona in South Sweden March 10th, in the neighbourhood of Stockholm about April 6th, etc.) the hazel pollen grains often fall on bog surfaces which at the moment can retain them only in a slight degree or not at all. I will quote one concrete example to show the importance of this. For some reasons the example is perhaps not very happily chosen—for instance, I have no meteorological data from the locality—but nevertheless it will serve to make clear my way of thinking.

At the base of a peat deposit near Inveroran in the Argyll Grampians, about 300 metres above sea-level, a "hazel forest" of boreal type is shown to have existed (hazel pollen frequency = 124 per cent.). In the younger layers of the deposit the hazel pollen frequency, as a rule, does not exceed 10 per cent. (diagram in *Geol. Fören. Förh.* Bd. 50, 184, 1928).

If hazel forests actually occurred at the present time in this neighbourhood, it would be doubtful whether the bog would really have the power to record their existence, if its youngest layer—which we assume to be living—should be prevented to any considerable extent by meteorological causes from catching and retaining pollen grains. On the other hand, the fossil pollen of the boreal layers of the bog, does not necessarily indicate that *real* hazel forests grew in the Inveroran country during the boreal period. As this period forms a part of the Late Quaternary warm period the great hazel pollen frequency might to some extent be due to the then earlier springs, during which the hazel pollen grains had a proportionally better chance than now of being caught and preserved in the bogs.

Early springs must have gone hand in hand with "climatic optima"; and in that connection it is interesting to note that the maximum frequencies of hazel pollen regularly appear in strata which are believed to have been laid down during a climatic optimum. In Central Europe this optimum is believed to be boreal (Bertsch, Keller, Rudolph, and others) and so are the hazel forests; in the Baltic countries the optimum would seem to be atlantic (von Post, Auer and others); in Russia either atlantic (Neustadt and others) or

sub-boreal (Dokturowsky). Moreover, during the last interglacial epoch of Denmark and north-west Germany, the maximum hazel occurrence seems to have coincided with a climatic optimum (Jessen). The British Isles alone form an exception to the rule, since the hazel pollen maximum, as has been previously mentioned, is not exclusively confined to boreal layers. But this may be due to the oceanic character of the climate, which makes the dead season of the bogs very short or possibly eliminates it altogether, thus rendering easier the catching and preserving of the hazel pollen. The hazel pollen maximum of the atlantic period in the Scottish islands seems to be due to historical causes, as the hazel did not reach those islands until the atlantic period (or possibly at the end of the boreal period). The gradual change of the climate during the atlantic period, and later, reversed the process of evolution; the forests were diminished or extinguished, and in the Shetland Isles only local *Salix* thickets persisted as a rearguard, just as in pre-atlantic times they acted as pioneers.

The Late Quaternary warm period is held to comprise boreal, atlantic, and sub-boreal times. In central Europe high hazel pollen frequencies are often found also in layers from the two later periods, especially the atlantic. Its predominance in boreal strata is connected with the fact that the hazel was very well equipped for the struggle for existence during boreal times, when the immigration, colonisation and consolidation of the forest elements and forests were still going on. That became more and more difficult during the succeeding periods, characterised by the slower modifications of the forests and keener competition, as the available areas became occupied by mature forest.

Boreal hazel forests have not as yet been proved to have existed in Russia. This can hardly be due, as in the Scottish islands, central Sweden and Finland, to historical causes, as, on the evidence of pollen statistics, the hazel occurred in Russia already in early boreal, possibly even in pre-boreal, time. The question why the hazel went back in Russia during the boreal period will here be left open. I think, however, that very probably the already mentioned Vistula-Dniestr line was particularly strongly marked during the boreal period: to the west of it there prevailed congenial conditions, short winters and long warm summers, to the east of it, in Russia and round the Baltic lake, not yet connected with the sea, the climate was probably even more continental than now. Therefore the activity of the peat-forming plant associations could only start comparatively late in the year, which would make it more difficult for the early flowering plants to be properly registered in the peat by means of pollen grains<sup>1</sup>.

<sup>1</sup> As to preservation in sediments these plants would be equally handicapped. In that respect the study of lines connecting the places where the ice-cover of the lakes breaks up at a certain date after the New Year would be of some interest. Thus, for instance, the line for the breaking up of the ice three months after the New Year runs from south Sweden south-eastwards through Galicia, Ukraine and across the lower course of the Dniepr to the Sea of Azov. I mention this



The increase of humidity during the atlantic period was a consequence of the inundation of wide areas in what is now the southern part of the North Sea and the establishment of a connection between that sea and the Baltic.

These changes made the Vistula-Dniestr zone less important as a climatic divide and consequently, as has previously been mentioned, the maximum hazel pollen frequencies east of this zone are encountered in atlantic and sub-boreal layers, which in its way may be an index of increased humidity.

Lack of space prevents me from going into details or from dealing with some problems closely related to my theme, as for instance the behaviour of *Alnus incana*, which flowers almost as early as the hazel, or the appearance of pollen

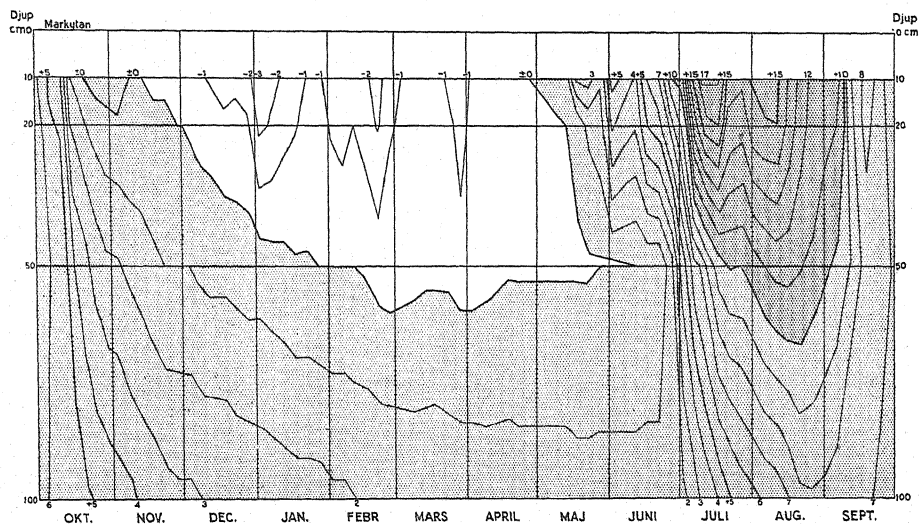


FIG. 2. Geothermoisoplethes from the Gisselås bog, October 1926–September 1927 (from BOOBERG). Djup cm. = depth in centimetres. Markytan = bog surface. Temperatures ranging between  $-3^{\circ}\text{C}$ . ( $+26.5^{\circ}\text{F}$ .) and  $+17^{\circ}\text{C}$ . ( $+63^{\circ}\text{F}$ .).

grains of *Tilia*, etc. in northern Finland, the Peninsula of Kola, and Novaya Zemlya, in places where the more transportable hazel pollen grains have not been found.

In conclusion I should like to emphasise the desirability of investigations, comparative and experimental, as to the possibility of catching and preserving pollen grains under extreme conditions of climate, especially at the limit of tree or forest growth. Until this is done, the scanty pollen flora of the oldest

detail here because such lines, no less than phytophenological lines showing the reaction of the plant world to the sum of the climatic factors, ought to be considered more than is usual at present. From the standpoint of pollen statistics, and especially in connection with the theme of this paper, a better knowledge of the yearly changes of temperature at different depths in the peat is much to be desired. Fig. 2 shows the geothermoisoplethes from the bog of Gisselås in North Sweden,  $63^{\circ} 42' \text{N}$ . lat.,  $16^{\circ} 21' \text{E}$ . long. (After BOOBERG, *Norrländskt Handbibliotek*, Bd. 12, Upsala, 1930.)

Late Quaternary deposits cannot be properly interpreted. It is also much to be desired that the well-established results of statistical investigations of pollen from the younger strata should be connected with the conclusions which can be drawn from the present actual and potential distribution of other biota than forest trees, not forgetting cryptogams and invertebrates. This would be entirely in the spirit of the botanical pioneer of pollen statistics, Prof. G. Lagerheim, and would pave the way towards a broader, deeper and less one-sided knowledge of geobiological development during Late Quaternary times.

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STOCKHOLM, *April* 1930.

# A CONSIDERATION OF SOME EXTERNAL FACTORS GOVERNING THE PRODUCTION OF PLANKTON IN THE SEA

By H. R. SEIWELL.

(With five Figures in the Text.)

## I.

STUDIES on the quantitative distribution of marine plankton have revealed that the degree of wealth of organisms varies from one region to another. The unicellular algae, by virtue of their chlorophyll, are capable when exposed to a sufficient amount of light of forming organic substances from water, various dissolved salts and  $\text{CO}_2$ . Plants are the "primary food" of animals and the more rapidly they form organic substances, the more animals they can support.

The external factors governing the production of marine phytoplankton have been divided by Brandt (5) into three categories, as follows: nutritive factors proper, general conditions of life, and indirect factors of production. It is the first and last of these divisions with which this paper is concerned. The first includes nutritive factors such as light, heat, inorganic food substances, etc., on which the speed of growth depends. The last, or indirect factors of production, do not in themselves control the nutrition of the plankton, but are responsible for its presence, or absence, within the limits of phytoplankton utilisation.

The compounds of nitrogen and phosphorus, essential to the protoplasm of both plants and animals, are represented in extremely small, often barely perceptible, traces in the sea and are considered foremost of the minimum substances. The extremely small amounts in which these substances are present in sea water may be visualised when it is noted that Matthews (1), using the purest chemicals, was unable to prepare artificial sea water containing less than 28.6 mg. of  $\text{P}_2\text{O}_5$  per cubic metre, an amount which is a little less than the winter maximum value at station E 1 in the English Channel. In the open North Atlantic (latitude  $63^\circ$  N. to  $11^\circ$  N.) the largest quantities of phosphate were recorded from the deeper water of the tropics and were well under 200 mg. per cubic metre, or less than two-tenths part per million (23).

In the upper illuminated layers of the ocean the intense photosynthesis will tend to bring about an exhaustion of the minimum substances unless replacement takes place. A certain amount of phosphate and nitrate is continually

being supplied from the excreta of the living organisms. The dead plants and animals sink into the lower layers, where they are devoured or transformed by bacteria into inorganic substances. These inorganic foods cannot be utilised by the bottom living organisms, and are brought up into the photic layer by vertical currents or processes of diffusion.

The greatest quantities of nutrient salts are in the abyssal regions of the deep oceans; this being especially the case in the tropical parts of the oceans where the deep layers are restrained from rising to the surface and manurial substances have accumulated in relatively enormous quantities. Harvey (7), on the basis of a series of nitrate and phosphate determinations below 100 metres at a position some 200 miles west of Portugal, has calculated that the dark depths of the three great oceans contain some 250,000 tons of nitrate nitrogen, and 75,000 tons of phosphate reckoned as  $P_2O_5$  which are lost to the cycle of events for an almost indefinite period. More recent observations on the phosphate content of the deep water of the open Atlantic (23, 6) have shown that phosphate is frequently present in the deeper layers in larger quantities than found by Harvey off the Portugal coast, so that actually there is probably more present in the abyssal regions of the oceans than his calculation shows. Nevertheless, the magnitude of Harvey's figures give an idea of the enormous quantities of nutrient salts which must be present in the greater depths of the oceans.

The abundance of manurial substances in the water of inshore areas varies with geographical location and local hydrographical conditions. In inshore areas where incursions of decomposed organic materials occur through drainage or other run-off, there will be a greater abundance of manurial substances than in an area in which there is no external supply. In other regions, as on the western coast of North America, because of up-welling water, the sub-surface layers are elevated and manurial substances enrich the photic zone. There are some inshore areas, however, in which no great amounts of manurial substances are brought into the photic zone through external agencies. In these areas at certain seasons the rate of utilisation of the nutrient salts may exceed the rate at which they are being returned to the water until one or more are in minimum, and then photosynthetic activity is greatly slowed up or even stopped until more nutrient material can accumulate.

## II.

The vital necessity of the presence of certain dissolved salts in the water for the production of vegetable plankton has been demonstrated by the regular seasonal changes of these substances observed to occur in relation to outbursts of phytoplankton in the English Channel (1, 2, 3, 7). In this locality it has been found that the entire water column averages some 60 to 70 mg. per cubic metre of nitrate nitrogen during the winter months. In the spring this con-

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centration is rapidly decreased, and by August the nitrate has been practically used up throughout all depths.

A similar seasonal variation has been noted for phosphate in the English Channel (Fig. 1) and water containing 30 to 40 mg.  $P_2O_5$  per cubic metre in winter is almost depleted of phosphate in the summer. The depletion occurs first in the upper layers when sunshine begins to exceed 3 hours a day, and the time varies from year to year. Toward the end of summer sunlight decreases, and phosphate begins to be reformed from dead organisms in the bottom water faster than it can be utilised by the phytoplankton. Vertical mixing in the

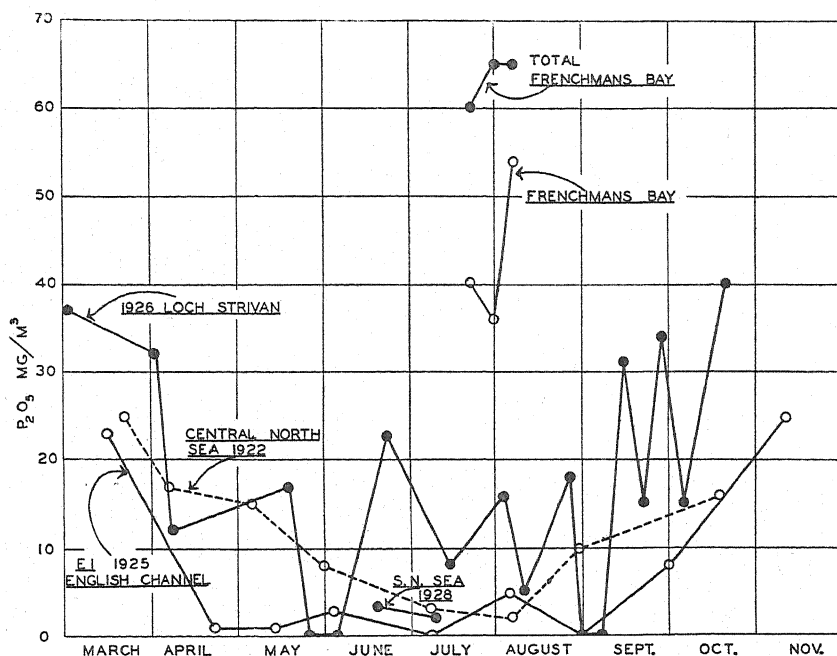


FIG. 1. Observed variations of  $P_2O_5$  in mg. per cubic metre, during the period March to November, in the surface water of Loch Strivan (13), central North Sea (4), English Channel (3), southern North Sea (20, 21) and Frenchmans Bay (surface and average of whole bay (18, 22)).

fall replenishes the surface layers, and this phosphate is utilised during the following summer. The phosphate in the bottom water is reduced to about one-third of its winter value (7). Similarly, Marshall and Orr (13), working in the Clyde sea area, found a close relation between diatom increases and fluctuation of dissolved phosphate (Fig. 1).

The occurrence of any one of the vital substances in minimum will limit the production of phytoplankton. Thus Harvey (8) has shown that in the English Channel during the summer months an increase in phosphate tends to occur when photosynthetic activity is limited, because of lack of nitrate, and *vice versa*.



Other observers have noted a seasonal variation of manurial substances in the surface water layers. Brandt and Raben (7) found a seasonal variation of nitrate in the North Sea owing to its utilisation by algae in the summer months. Thompson (24) has noted a marked seasonal variation of phosphate and silicate in the Puget Sound region, the greatest variations being obtained in the spring and summer; and Moberg (15) has found occasional seasonal variations of organic nitrogen and phosphate in the waters of the southern California region.

### III.

In regions such as the English Channel, where there is no great influx of nutrient materials through external sources and where the water is sufficiently shallow, so that photosynthetic activity can extend throughout the whole column of water, the phosphate content of the whole water mass will be greatly reduced by the end of summer. In the shallow North Sea, where the depths are generally less than 100 metres, and where an appreciable temperature difference ( $7^{\circ}$  to  $8^{\circ}$ ) may exist between surface and bottom in summer, thus denoting an absence of vertical mixing, the nutrient materials are more or less utilised throughout the whole column of water by the end of summer (Fig. 1).

Thus we find that Atkins (4) on July 6th, 1922, near the centre of the North Sea, recorded 3 mg./m.<sup>3</sup>  $P_2O_5$  for the surface water and 5 mg./m.<sup>3</sup>  $P_2O_5$  for the bottom water at a depth of 50 metres. The author (20), while working in the southern part of the North Sea, mean latitude  $52^{\circ} 34' N.$ , June 18th to 22nd, 1928, recorded an average value of 3.44 mg./m.<sup>3</sup>  $P_2O_5$  for the surface water and a few weeks later (July 8th to 11th) (21) recorded values varying from 0.6 to 3.1 mg./m.<sup>3</sup>  $P_2O_5$  for the surface water of the North Sea on a line between the mouth of the Elbe River and the Shetland Islands. Near the centre of the North Sea the surface water was practically exhausted of phosphate (Fig. 1).

In the deeper parts of the North Sea off Norway, where the depth may extend below the limits of plant activity, and where the surface layers are warmer than they are in the water farther off shore, there is more resistance to vertical mixing in the summer and phosphate may then accumulate in the deeper layers below the reach of photosynthetic activity. Thus, on August 30th, 1924, at  $57^{\circ} 51' N.$  latitude and  $6^{\circ} 39' E.$  longitude, off Norway, Atkins (4) found that the deeper water was not denuded of phosphate, as much as 42 mg./m.<sup>3</sup> being recorded at 300 metres.

### IV.

The phosphate content of the shallow surface water in the vicinity of the Shetland and Faero Islands on July 11th and 12th, 1928, was found to be 5 to 8 mg./m.<sup>3</sup>  $P_2O_5$  while for the surface water in between (Faero-Shetland Channel) values as great as 34 mg./m.<sup>3</sup>  $P_2O_5$  were recorded (21). The differences



in phosphate content are obviously brought about by vertical mixing. The thin layer of water overlying the Faero and Shetland Banks is in summer heated to a higher temperature than the surrounding water: thus it becomes lighter,

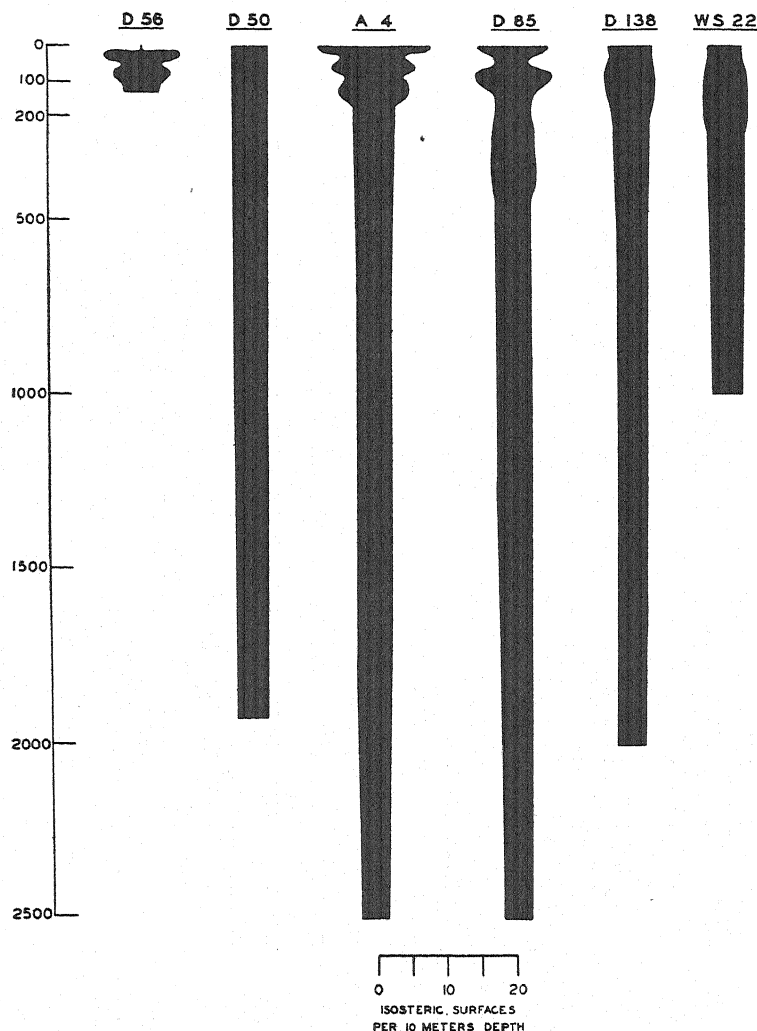


FIG. 2. Vertical stability of the open North Atlantic Ocean from south of Iceland to latitude  $53^{\circ} 38' S$ . The width of the columns is proportional to the degree of stability (see text, pp. 169, 172, 174).

and an interchange of water between it and deeper rich phosphate layers is prevented. On the other hand, in the Faero-Shetland Channel, eddy movements resulting from the velocity of currents produce a mixing of the surface and subjacent layers which tends to enrich the surface layers with phosphate as well as other manurial substances.

Similarly over the Faero-Iceland Ridge the surface layers are enriched by vertical mixing, and amounts of  $P_2O_5$  as great as 25 mg./m.<sup>3</sup> were recorded in midsummer of 1928 (21).

It is obvious that in regions such as the Faero-Shetland Channel and the Faero-Iceland Ridge, the surface layers should be kept supplied with phosphate throughout the season of greatest phytoplankton activity.

In the surface water 15 to 75 miles off the south coast of Iceland, July 15th to 19th, the phosphate content ranged from 6 to 20 mg./m.<sup>3</sup>  $P_2O_5$ : in general the phosphate content of the surface water was highest where the water was deep and farthest from shore (21). Here again the phosphate in the surface water appears to be largely dependent on vertical mixing with the richer underlying layers, and as an indication of the stability of the water mass south of Iceland, in relation to distance from shore, the stability calculated from the data observed by the Danish investigators in May 1896 (11) is illustrated in Fig. 2 (see method of stability calculation described by Sandstrom (19)). The stability of the shallow water at station D 56, 15 miles off shore, is greater than that at station D 50, about 90 miles off shore. In July we should expect the stability of the upper 100 metres to be somewhat greater than indicated on account of greater solar warming. Nansen (17) has shown that, in the sea south of Iceland, cooling of the ocean's surface may produce convection currents extending to a depth of nearly 800 metres, although in July the effect of this circulation is less marked in the upper 100 metres on account of solar warming.

Observations on the phosphate content of the surface water overlying very deep strata do not always give an indication of the amount of phosphate in the photic zone available for plant utilisation. As an example, at a station off the south-east coast of Iceland (latitude 63° 30' N., longitude 14° 41' W.) 10 mg. per cubic metre of  $P_2O_5$  were recorded for the surface water, but at a depth of 100 metres 40 mg. l m.<sup>3</sup>  $P_2O_5$  were available for plant utilisation (21). Similar results have been obtained by the author from parts of the equatorial Atlantic where the surface waters were almost exhausted of phosphate, 3.5 to 5 mg./m.<sup>3</sup>, yet at 100 metres there were quantities ranging from 41 to 90 mg./m.<sup>3</sup>  $P_2O_5$  (23).

## V.

On the eastern coast of North America the observations of the Canadians in Passamaquoddy Bay and of Rakestraw in Frenchmans Bay indicate that in both of these bays, where moderately strong tidal stirring occurs, the waters were well supplied with phosphate during the summer months. Summarising the chemical observations of Rakestraw (18) we find that during the period July 20th to August 6th, the phosphate present in the surface water averaged about 46 mg./m.<sup>3</sup>  $P_2O_5$  while that for the whole bay was about 66 mg./m.<sup>3</sup>  $P_2O_5$ . It is also interesting to note that in this Bay the average phosphate content of the surface water increased from 40 mg./m.<sup>3</sup>, July 20th, to 54

mg./m.<sup>3</sup> on August 3rd, and the average P<sub>2</sub>O<sub>5</sub> content of the whole bay increased from 60 to 65 mg./m.<sup>3</sup> (Fig. 1).

Nitrate observations in the bay gave a general average of 36.3 mg./m.<sup>3</sup> N for the season and indicated that, as with the phosphate, this material was supplied to the water at a greater rate than it was utilised by plant activity throughout the summer observational period. The observed range of average nitrate content, calculated as N, of the water in the bay was 35.6 mg./m.<sup>3</sup> July 20th to 41.3 mg./m.<sup>3</sup> August 3rd. The greatest depths of Frenchmans Bay are well under 100 metres.

In Passamaquoddy Bay, which is stirred to an even greater extent than Frenchmans Bay (22), it is probable that the manurial content of the water is high in summer. This, at least in the case of phosphates, seems to be indicated in a letter from Dr Huntsman (9) from which we assume that phosphate determinations in this Bay during summer gave results in the neighbourhood of 30 mg./m.<sup>3</sup> P<sub>2</sub>O<sub>5</sub>.

On the western coast of North America, Moberg (15), working in the La Jolla region, has found that at the surface phosphate generally varied from 25 to 35 mg./m.<sup>3</sup> P<sub>2</sub>O<sub>5</sub>, and in the summers of 1924 and 1926 it fell to 15 or 20 mg./m.<sup>3</sup> P<sub>2</sub>O<sub>5</sub>; in 1925 he observed no such change. This last author, in illustrating the chemical and physical conditions of the water at a station 10 miles off the coast of southern California during the summer of 1926 (16), showed that all the conditions determining the environment of the phytoplankton varied greatly with depth. The important chemical substances silicate, phosphate and carbon dioxide, were present in sufficient quantities for phytoplankton activity in the surface water, only nitrate was lacking in the upper 25 metres. However, below 25 metres this latter substance increased rapidly with depth, and was abundant at 30 to 35 metres below the surface, a zone to which the diatoms were principally confined. It is possible, that above 25 metres, nitrate may have been a limiting factor in diatom production.

The presence of nutrient materials in the upper layers of the southern California region is almost entirely the result of vertical circulation caused by up-welling of the sub-surface layers. Moberg has pointed out that decomposition of organic material takes place at or near the bottom and the products, in the form of nutrient materials, are returned by up-welling water to the photic zone of plant activity where they are utilised. Because of slight rainfall and absence of rivers on this coast, no manurial substances are supplied to the water from the land as is probably the case in Frenchmans and Passamaquoddy Bays.

Up-welling off the coast of California has been demonstrated by McEwen (14) who found that the rate of up-welling varies with season and locality, and Moberg (16) has shown that practically all factors influencing the environment of the phytoplankton, with the exception of light, are affected by up-welling.

Obviously, then, the distribution and magnitude of the diatom production off this coast depends on the amount of up-welling.

Thompson (24) and his co-workers at the Puget Sound Biological Station have found that the phosphate content of the waters in that region averages between 0.14 and 0.16 mg.  $P_2O_5$  per litre, or 140 to 160 mg.  $P_2O_5$  per cubic metre, while silica averages about 2 mg. per litre or 2000 mg. per cubic metre  $SiO_2$ . The phosphate data agree with those obtained at depths of 150 metres off the coast of southern California.

## VI.

The chemical fertility of the open ocean depends principally on the abundance of dissolved phosphate and other manurial substances in a thin upper stratum of the water column at depths where they can be utilised by the phytoplankton. It has previously been pointed out that the abyssal regions of the oceans contain enormous stores of manurial substances, but that they are lost to the cycle of events until transported into the photic zone of plant activity. Consequently, it is not the amount of nutrient material in the deeper parts of the oceans, but rather the presence and magnitude of vertical ascending currents which transport manurial substances into the layer of plant activity that influence the environment of the vegetable plankton (Fig. 3).

Investigations on the phosphate content of the surface waters of the open sea have shown that this substance varies considerably from place to place. In general, the phosphate ( $P_2O_5$ ) content of the surface water ranges from almost complete exhaustion to more than 100 mg./m.<sup>3</sup>, while below 750 metres phosphate is generally present in quantities greater than 50 mg./m.<sup>3</sup> (23). In the high latitudes of the open ocean, because of increased number of hours of sunshine, plankton attains its greatest development in spring and summer. In these regions the manurial content of the surface layers drops or even becomes exhausted during the flowering seasons unless there is replacement of that which is utilised.

In the northern part of the North Atlantic, surface values ranging from 15 to 22 mg./m.<sup>3</sup> or more have been reported for the summer months; while in the tropical parts of this ocean as little as 3 mg./m.<sup>3</sup> have been recorded (23). In high latitudes, where there is less restraint to vertical circulation, the photic zone of plant activity may be frequently replenished with manurial substances from the deeper layers, while in lower latitudes vertical ascending currents are restrained from rising to the surface and the manurial substances often accumulate in the deeper layers while the surface layers become exhausted (Fig. 3, C 9). There are large areas in the tropical parts of the oceans where the photic layer of plant activity is never abundantly replenished with nutrient salts.

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As an indication of the resistance of the water column to vertical mixing in arctic and tropical latitudes attention is called to Fig. 2. Fig. 2, D 50, represents the uniform stability of the water south of Iceland as calculated from the results of the Danes in May 1896 (11), and figure A 4 the stability

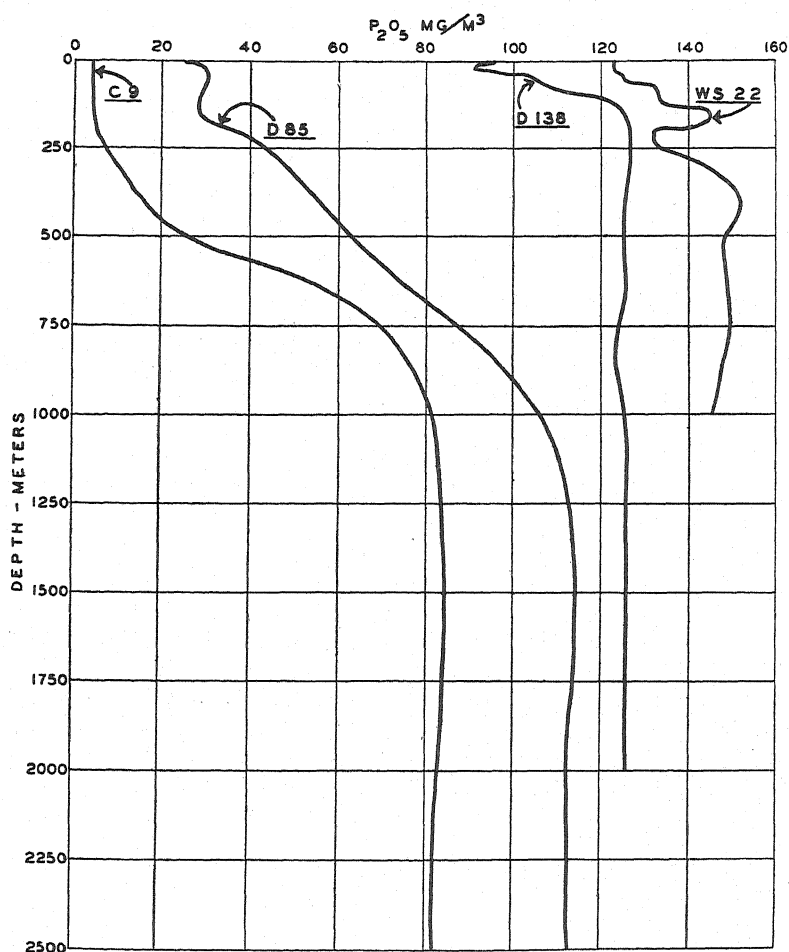


FIG. 3. Vertical distribution of phosphate as  $P_2O_5$  in the open North Atlantic from the Tropics to the Southern Ocean (see text, p. 174).

of tropical water at about latitude  $27^\circ$  N. and longitude  $35^\circ$  W., as calculated from Jacobsen's average hydrographical data for atlantic "area 4" (10). The development of resistance to vertical circulation, or the stability of the vertical column, is indicated by the widening of the vertical. In the former region evidence that the photic zone was well supplied with phosphate was indicated, by recording 20 mg./m.<sup>3</sup>  $P_2O_5$  for the surface water in mid-summer of 1928 (21),

while in the latter region the phosphate content of the upper 200 metres was not over 5 mg./m.<sup>3</sup> P<sub>2</sub>O<sub>5</sub> (23) (Fig. 3, C 9).

In the region of the equatorial Atlantic there is a marked up-welling of water from the lower levels to replace the surface water driven polewards by the combined effect of the trade winds and the earth's rotation. Consequently, the phosphate content of the photic layer in this belt of up-welling stands out in decided contrast to other parts of the impoverished tropical Atlantic, and values up to 90 mg./m.<sup>3</sup> have been recorded for the 100 metre level.

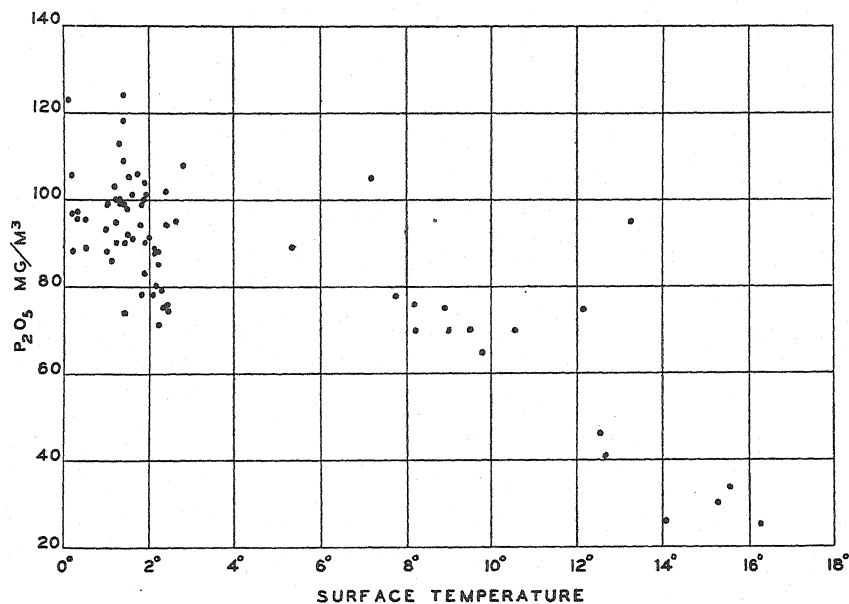


FIG. 4. The distribution of surface phosphate values in relation to temperature of the surface water in the South Atlantic Ocean. Graph drawn from observations of 'Discovery' expedition (6).

The differences in chemical fertility of the North Atlantic as briefly outlined find a correlation with the summer quantities of phytoplankton as determined by Lohmann (7, 12). In the deep ocean, far from land, the animal and plant plankton in tropical and sub-tropical latitudes was found to be considerably less than in higher latitudes, although the phytoplankton between 10° N. and the equator was greater than that found to exist between 30° and 10° N.

## VII.

The recent hydrological investigations of the 'Discovery' expedition (6) in Antarctic waters have revealed that the quantities of inorganic phosphate in solution in the surface layers of this region are enormous when compared with what has been recorded for other regions. Seventy-three vertical series



of phosphate determinations were obtained between latitude  $33^{\circ} 08' \text{ S.}$  ('Discovery' station 85) and latitude  $55^{\circ} 20' \text{ S.}$  (W.S. station 36); the phosphate content of the surface water ranged from 25 to 144  $\text{mg./m.}^3 \text{ P}_2\text{O}_5$ . In Fig. 4 a plotting of surface observations against temperature indicates that, in general, the largest quantities of phosphate occurred in the colder surface water in the southern part of the region investigated. The lowest value, 25  $\text{mg./m.}^3$ , was observed at the most northern station (85) and the highest at latitude  $53^{\circ} 45'$  (station 124).

Fig. 2, D 85, D 138 and W.S. 22 illustrate differences in stability of the water columns, and Fig 3, D 85, D 138 and W.S. 22 the vertical distribution of phosphate in the region investigated. Here again we see that as in the case of the North Atlantic the least resistant water occurs in the high latitudes, and coincident with the greater vertical mixing there are larger amounts of phosphate in the surface strata. In the high latitudes of the South Atlantic Ocean where the temperature range of the water column may be of the order of 2 to 3 degrees ( $0.55^{\circ}$  to  $2.02^{\circ}$ , 0 to 2000 metres at station 138) a small drop of surface temperature will produce vertical mixing to a greater depth than would be the case in the lower latitudes where the temperature range of the vertical column may be 16 or more degrees ( $1.01^{\circ}$  to  $16.26^{\circ}$ , 0 to 4800 metres at station 85).

Fig. 5 represents the phosphate from surface to bottom in a section extending in a south-westerly direction from 'Discovery' station 85 (latitude  $33^{\circ} 08' \text{ S.}$ , longitude  $4^{\circ} 30' \text{ E.}$ ) through 'Discovery' station 7 (latitude  $39^{\circ} 25' \text{ S.}$ , longitude  $12^{\circ} 08' \text{ W.}$ ), station 9 (latitude  $46^{\circ} 12' \text{ S.}$ , longitude  $22^{\circ} 28' \text{ W.}$ ) to station 11 (latitude  $50^{\circ} 26' \text{ S.}$ , longitude  $30^{\circ} 27' \text{ W.}$ ).

At the northernmost station, 85, the most stable water and greatest changes in phosphate occurred above 1000 metres; below this level the phosphate content was practically uniform. Farther south the phosphate content of the surface layers increased and became more uniform above 1000 metres. On the other hand, in the deeper water of the southern part of the section, the phosphate gradient increased and at the most southerly station, 11, we find 209  $\text{mg./m.}^3 \text{ P}_2\text{O}_5$  at 4500 metres depth. This quantity is much greater than has been found for the water of the North Atlantic, and illustrates the extreme wealth of nutrient material in the Southern Ocean.

#### VIII. SUMMARY.

The compounds of nitrogen and phosphorus are considered the foremost of minimum substances in the sea. They are present in minute, often barely perceptible traces, very rarely in excess of two-tenths parts per million. Relatively large quantities of nutrient salts are present in the abyssal regions of the sea, but they are lost to the cycle of events until transported into the upper illuminated layer of photosynthetic activity. In the upper illuminated layers of the ocean an intense photosynthesis will bring about an exhaustion of the minimum nutrient materials unless a replacement occurs. This replace-

ment is brought about chiefly by vertical ascending currents transporting nutrient materials from the deeper layers.

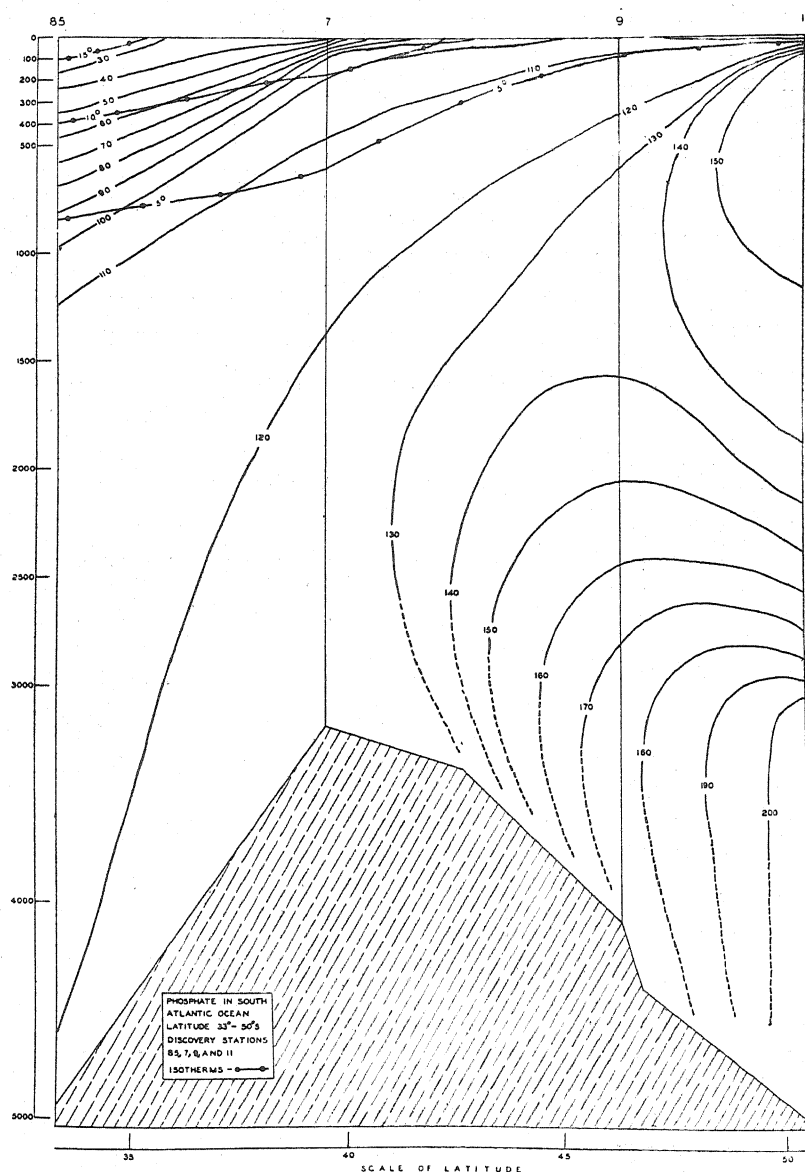


FIG. 5. Phosphate in the South Atlantic Ocean between latitude 33° S. and 50° S. from observations at 'Discovery' stations 85, 7, 9 and 11 (6) (see text). Equal phosphate lines are drawn for every 10 mg. of  $P_2O_5$  and isotherms for 5°, 10° and 15°.

The chemical fertility of the open ocean is principally dependent on the hydrographical characteristics of the region. In the cold water of high latitudes

the water is less resistant to vertical mixing than it is in the tropics, and consequently there is more nutrient material available for plankton utilisation.

Quantitative investigations of dissolved inorganic phosphate in the Southern Ocean have revealed that the great wealth of this substance in that region is sufficient for an enormous vegetable plankton population during the summer months.

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## THE STANDARDISATION OF DESCRIPTIONS OF PLANT COMMUNITIES<sup>1</sup>

By E. J. SALISBURY.

PROF. PAVILLARD once wrote "all is difficult in Phytogeography except the construction of artificial systems or the invention of new names." The task before me is neither concerned with a new system of classification nor with a new terminology but with the consideration of those features and characteristics which may be regarded as essential to the adequate description of a plant community. The most sanguine person could scarcely hope for unanimity on this subject, but nevertheless this presentation of my personal views as to what is essential in general, or in particular desirable, may serve as a basis for discussion in arriving at an agreement on what, in the general consensus of opinion amongst ecologists, should be regarded as requisite to the proper diagnosis and delimitation of vegetation units.

If our descriptive ecology is to advance knowledge and not to degenerate into a mere cataloguing of observations it must aim at discovering the causal relations which determine the character and structure of the communities we study. The problem is necessarily a complex one because of the many factors involved and the intricacy of their interaction. The method of abstraction involved in most experimental studies is inadequate alone but must be supplemented by comparative studies of communities which, however, are only valid when comparable data are available.

If we ask what are the communities we wish to compare, the answers will perhaps be as varied as the ecologists questioned. There would, however, probably be common agreement that they are not stable entities, but represent stages in continuous successions. Even when we are able to arrange our communities in a definite sequence with considerable certainty, which is often not possible, the constituent phases quite commonly appear in nature as naturally separable units, whilst their connection is often obscure or only theoretically probable. We therefore rarely do violence to the actualities by treating these phases as separate abstractions, since their separation is often more evident than their connection.

Each succession series can clearly be viewed as a whole, and a comparison made between entire successions, or we can compare the constituent phases of one succession with those of another. A very large number of successions tend to form a series of phases separable into three aspects, viz. the therophytic, the herbaceous, and the phanerophytic, each of which may, by climatic

<sup>1</sup> This paper opened the discussion on this subject at the International Botanical Congress at Cambridge, August, 1930.

or edaphic conditions, be established as a climax or sub-climax. For example, the first as desert or the therophytic communities of sand dunes, the second as grasslands, the third as scrub or forest. But where all these phases are present in the same succession it is clear that, studied as communities having a more or less definite physiognomy and structure, there is more in common between the grassland communities of different successions than between the various phases of the same succession, and whereas phases of different successions may be directly comparable in their entirety, the successions as a whole may not.

A complete succession is rarely, possibly never, stereotyped, but is subject to variation, so that the succession as a whole is necessarily more complex than its constituent parts, and the relation between cause and effect consequently more difficult to unravel. Hence comparison between the constituent phases is likely to yield information as fundamental as comparisons between successions as a whole. Comparison between different phases of the same succession, and between physiognomically comparable phases of different successions, may alike be expected to yield important results, and both are essential to the scientific study of the community and are mutually complementary. To employ an entomological simile, we can compare larva with larva, pupa with pupa, or imago with imago, or we can essay the more difficult task of comparison between the entire life histories. Whatever our particular predilection, the unravelling of the web of cause and effect can only be accomplished by a comparative study which, at least, takes cognisance of all the major factors of the environment and the significant features as to structure and composition of the community.

Everyone who has utilised a flora must have experienced the difficulties, especially in more critical genera, arising from the lack of uniformity in description. Much that should be explicitly stated is often left to be inferred, whilst quite frequently the characters upon which stress is laid with respect to one species have not been examined with the same critical care in its immediate allies. This, which is true of the individual species, is perhaps even more true of the communities which they form.

The history of plant ecology has passed through many, if not most, of the vicissitudes which have marked the progress of taxonomy. Indeed it is perhaps not too much to add that if, in the classification of plant communities, we have on the one hand gained inspiration from the methods of taxonomy, we have on the other hand shared some of its past defects and present faults. The plant community is the species, or it may be the genus, of the synecologist and, in common with the systematist, we are confronted with the same difficulties as to the limits of the aggregates of which we treat.

The taxonomist recognises that his species include a number, sometimes a very large number, of pure lines, of races differing by one or more unit Mendelian characters, and including perhaps several varieties or sub-species.



The species is invariably an aggregate, not merely of individuals but of ecotypes and strains, and the size of that aggregate depends very largely on the point of view of the investigator. Whether we apply the term species to the Linnean or to the Jordanian is ultimately a matter of convenience. The species itself is, in fact, an aggregate of convenience of which the members conform more or less closely to a predetermined type. When we attempt to define the species more precisely we find ourselves confronted with aggregates of inconvenience which render nomenclatorial confusion worse confounded.

The synecologist is similarly confronted with the choice between large aggregates such as those of Swiss phytosociologists and small such as those of the Upsala school; but, as with pure taxonomy, I venture to think that the size of the aggregate that we recognise is relatively unimportant so long as its delimitation and description be clear and accurate. It is, however, essential that there should be a basic uniformity in such descriptions which, whilst facilitating comparison between the results of various investigators, would in no way militate against individual initiative, so essential in a juvenile subject like our own.

At the present day there are various schools of thought in ecology, each dominated by a particular direction of approach. Floristic ecology, physiognomic ecology, edaphic ecology and successional ecology have all produced systems of classification which have little in common, except a certain exclusiveness with respect to points of view other than their own. Such an exclusiveness is almost inevitable when so many communities have been investigated mainly from a single aspect.

It should clearly be the aim of our synecological classification to express the sum-total of our knowledge with respect to communities, and such an ideal can only be realised when comparable data are available respecting the basic facts of every type. No one perusing the current literature of to-day can fail to recognise the frequent impossibility of proper comparison between descriptions of communities by various authors, when some aspects are entirely ignored or but very superficially treated, whilst in other instances the author has been so obsessed by a particular point of view that important facts of structure and floristic composition pass unrecorded, or are lost in polemical considerations.

The ecologist is unfortunately debarred in most cases from preserving type specimens of his phytosociological species, though in this connection it may be suggested that the citation, in descriptive monographs, of comparable communities where present in national reservations, might serve a useful purpose. As, however, this is only possible in a small proportion of the world's communities and as even the most stable community is subject to secular change, the necessity of adequate and fundamentally comparable descriptions is even greater than in the case of individual species.

The only satisfactory remedy would appear to be the standardisation of



description of communities, a generally accepted framework which, whilst tending towards uniformity of data, should neither hamper initiative nor restrict originality of treatment. It is only in this spirit of, I hope, helpful suggestion that I have ventured to select such data as would appear to be generally desirable. Such a scheme will doubtless require modification, but it should not be beyond the ingenuity of ecologists to arrive at some common denominator of their diverse methods of approach which would not be so exiguous as materially to diminish its utility. The work of recent years has afforded abundant evidence of the interaction of organisms and their environment, so that I shall assume there is no longer any question of describing communities in terms of their vegetation alone or of ignoring the influence of the organisms in modifying the environment which they occupy.

The adequate delimitation of the community can be regarded as comprising four categories of data which, though necessarily interrelated and overlapping, can, without undue sacrifice of reality, be considered as separate abstractions. These categories are the physiognomy, the floristic composition, the environmental factors, and the successional changes. Of these the last, however important for purposes of classification, are in a different category with respect to diagnosis, since the time factor involved often precludes the possibility of actual observations, in consequence of which, the successional data are commonly a matter of interpretation rather than observation. It will be convenient to consider each of these aspects in turn as a means of characterising the community, but it is fully realised that the distinction between them is indefinite, and consequently their grouping is to some extent a matter of personal preference.

#### PHYSIOGNOMY.

Physiognomy has long been recognised as an important characteristic of the plant community, and since the physiognomic features do in great measure reflect the natural sorting out of species in relation to the totality of the environmental conditions, it is not too much to say that physiognomy is the most important of the features to be defined in describing a plant community. Two difficulties, however, are chiefly responsible for the meagreness of our data on this point. These are, firstly, that communities are not static but dynamic, and that consequently the physiognomy at a given time is not necessarily in equilibrium with the contemporaneous environmental conditions. This difficulty presents something of a parallel to the confusion that arises when two closely allied species hybridise together, and the specific limits are obscured by the continuity of the transitional forms. The constituents of the transition community can only be separated by critical study, but the failure of physiognomy in such instances to analyse the community complex is rather its justification than its condemnation.

The second difficulty is the more serious, and depends on the inadequacy

of morphological and physiognomic nomenclature. The first requisite for the definition of physiognomic character is the description of structure. This necessarily implies the recognition and delimitation of the partial communities (corresponding to the partial habitats into which the community as a whole can be resolved). In a woodland, for example, the stratification of shoot systems and root systems, the assimilatory periods and seasonal changes of the overground organs, are necessarily involved in such description of structure. As I have elsewhere indicated (*Schroeter Festschrift*) what is involved in the concept of structure as applied to woodlands, I need not elaborate the topic here. But it may be emphasised that the average area occupied by the constituent units is an important feature of structure and can be readily measured by the method of Du Rietz. Height and area are together the nearest approach we have to numerical designation of form. The combination of height and area into one figure representing average volume, though perhaps useful in special cases, is fraught with considerable danger, since height and area are not interchangeable in respect to their phytosociological significance. The sociability of species is in reality a physiognomic factor and, where pronounced, is equivalent to an increase in the area occupied by the individual. As I have already pointed out with regard to woodland species, such marked social habit is at once a means of protection and aggression.

Ecads should, in the author's opinion, be regarded as physiognomic features, for when present these habitat forms stand in the same relation to the physiognomy of a community as exclusive species do to the floristic composition; they are more or less exclusive physiognomic types, and their importance sociologically is similarly dependent upon the frequency of their occurrence and on their distribution.

Similarly the view is here taken that the life forms of the individual species of a community are an essential part of its physiognomy. The restriction of the concept of physiognomy to that of the dominants of a community is really to characterise the whole by a part that commonly represents a single stratum. The physiognomy of the dominants is often, in fact, that of a partial habitat. Individual treatment of partial habitats is often desirable, but the physiognomy of the community is an integration of the life forms of all its constituent members. Where there is marked stratification the strata should, however, probably be treated separately.

One cannot praise too highly the work of Raunkiaer in emphasising the importance of the life form of the individual species<sup>1</sup>. Nevertheless the very systems of classification which Raunkiaer invented to facilitate the study of these characteristics, and which should have led to an advance in our knowledge, have perhaps actually, by the formality of their application, led to a retardation and stagnation of our progress. The fact that *Vaccinium*

<sup>1</sup> The value of life forms for purposes of description of physiognomy is independent of the relation between form and habitat.

*myrtillus* is evergreen in one habitat, whilst in another it is a deciduous shrub which becomes a "switch plant" in winter, is of far more significance in the characterisation of the community than slight differences in the percentage of the diverse life forms. So too the annual duration of *Medicago lupulina* and *Scirpus setaceus* in some communities, and their perennial duration in others, features to which M. Allorge has drawn attention in the *Vexin français*, are differences which at once characterise the communities in which they occur. But too often the allocation of a species to a particular category of life form has been quite perfunctory and such important distinctions in behaviour have passed unheeded.

The height of the perennating organs of the constituent species is an important physiognomic character, but it is desirable that the elements of distinct partial habitats should not be confused. Moreover, it is essential that such data should be based on actual measurements sufficient to justify conclusions respecting the range observed and to establish means.

The formal simplicity of Raunkiaer's classes has rendered them easy to apply and widely accepted, but the large class intervals, on which this simplicity chiefly depends, is calculated to obscure rather than to reveal the differences in this respect between closely related types. In effect, the Raunkiaer classes are in practice qualitative rather than quantitative, and it is quantitative data of which ecology stands most in need. The forester is fully aware of the great value of form and height as a means of distinguishing the various categories of site, and indeed Büsgen goes so far as to state that in forestry height growth serves as the best measure of the quality of the locality.

There can be little doubt that such data could be made of equal value to the ecologist. Thus it is very significant, as a total measure of the environment, that one species of tree exhibits a frequency curve in respect to height with a particular mode and dispersion in one locality, whilst in another the mode and range are different. What is true of the phanerophytic vegetation is true also of herbaceous types, and indeed the species common to various communities are natural phytometers which, by their differences in height and growth, contribute to the respective physiognomy of each. In defining the physiognomy of the community it is, therefore, important to determine the range of variation of the constituent species collectively, and individually those which by their different response in different communities serve for the phytometric integration of the total environment. The range in height of the individual species may be emphasised by the therophyte *Linum catharticum*, which on chalk downland normally attains a height of from 5 to 50 cm., whereas as a member of the dune slack community it presents an ecad scarcely more than a centimetre in height. It is customary to adopt Raunkiaer's classification into Phanerophytes, Chamaephytes, Hemicytrophytes and Geophytes, and a specific spectrum of this character is of diagnostic value, but it fails to distinguish between the community with the species of a particular category

abundant in individuals, and another in which this biological type is represented by the same number of species but all of them of rare occurrence. It is clearly of significance if, in a community rich in species, one category predominates and the biological spectrum reveals this feature; but in addition we require determinations of the heights of the perennating organs based on actual measurements of a number of examples of each species and expressed in relation to the abundance of each. From the standpoint of the physiognomy of a community, there is but little difference between the community composed of individuals of one species or of several species all belonging to the same biological category. Such features could be expressed numerically as products of the respective mean heights and average abundances, or graphically with the mean heights as ordinates and the mean abundances as abscissae. For comparison of similar simple communities, or strata (in stratified communities), a single numerical value could be obtained expressing the mean average height by the sum of the products of the mean heights of all the species of a community with their respective average abundances divided by the sum of their respective abundances. Some such method of treatment appears necessary for giving greater precision and as far as possible quantitative expression to physiognomic characters.

The size of leaf of the constituent members of a community has been found a useful characterisation, but here, too, the value of the data would be greatly enhanced by being based on a more definite statistical treatment. In this connection it may perhaps be pointed out that the measurement of the areas of a large number of leaves is by no means a difficult task if a planimeter is utilised. The mode of the leaf area should be determined for each of the dicotyledonous species, and the mean value for the community or its several parts based on the average of all the species, having regard to their respective average abundances. In the case of communities dominated by Monocotyledons the width of the lamina is a useful index. The author has already shown that, if due regard be paid to the precautions necessary through variation in different parts of the organism as a whole and of the individual leaf, the stomatal frequency is a valuable indicator of the relation of the plant to its environment. This means of comparison is especially valuable where the same species is present in different types of vegetation or in successive communities of a sere.

The average number of individual plants per unit area and the average area occupied by an individual of each species may also serve as useful criteria for physiognomic comparison.

The importance of changes in the form of the individual is sufficiently emphasised by the case of *Pinus sylvestris* which, in northern latitudes and high altitudes, has a tapering crown, whereas in lowland and southern situations the crown tends to be flat-topped or rounded. Dr Kawada informs me that the same is true of *Cryptomeria japonica* in the northern and southern

portions of Japan. When such characteristic forms are present they should obviously be included in the description.

Even with respect to such obvious characteristics as the deciduous or evergreen nature of the chief species, data are often inadequate and the assimilatory periods of herbaceous types, though often quite characteristic, are but rarely recorded. These few examples suffice to show that physiognomic characters are capable of far more definite expression than they are usually accorded, and, whether a feature of the entire community or of a particular species, may be of considerable diagnostic value.

#### FLORISTIC FEATURES.

With respect to floristic constitution we are probably all agreed that a list of species as complete as possible, and preferably including both phanerogams and cryptogams, is an essential to adequate description. Most would also agree that the component species should be classified according to their constancy, exclusiveness, abundance (relative proportion of individuals) and frequency (dispersion), but, on the other hand, there will doubtless be considerable diversity of opinion as to how these should be determined and their relative importance.

For the statistical representation of the floristic composition of a community it is obvious that the data, if they are to be of any value for comparative purposes, must have some common basis.

In a very large proportion of descriptive accounts the observations are reduced to a percentage basis. This may actually be misleading, as it involves the erroneous assumption that the increase in each category, whether it be of biological types, exclusive species, constant species or any other class, is proportional to the increase in the total flora. For example, Braun-Blanquet found one therophyte (viz. *Moehringia trinervia*) as a constant constituent of the beechwood community of the Cevennes, of which the total flora numbered forty-seven species. Representation on a percentage basis involves the tacit assumption that at least two therophytes would be present as constants if a hundred species were involved. In communities composed of a small number of species the presence of aberrant or rare types becomes unduly exaggerated by percentage representation, whilst in tropical communities where large numbers of individuals of a single species are replaced by a diversity of species, departures from the mode may be unduly minimised.

The only satisfactory basis would appear to be that of *equivalent* areas such as 100 areas (of e.g. 1 sq. metre) each based on a random selection. These must, however, be in equivalent communities as judged by physiognomy, and it should always be definitely stated whether the data represent an aggregate of partial communities or a homogeneous assemblage.

The difficulty with respect to an arbitrary area basis is consequent upon the inadequacy of small unit areas in open communities such as deserts or in



communities of large trees. This demands variation in size of the unit areas not only for different types of community but for different communities in the same sere. Unless some arbitrary basis be adopted for this variation the numerical results can have but little significance. This difficulty might be overcome by multiplying the 100-unit areas and utilising the average of the several series as a basis of comparison (cf. however, below).

It might be argued that some definite basis of increase based on the probable increase of number of species with increasing area could be evolved.

It is well known that the number of species per unit area does not increase proportionally with the size of that area, but whilst at first the number of species augments rapidly, with further increasing size of the area studied the rate of increase falls off till the curve becomes well-nigh flat. The empirical formula suggested by Arrhenius has been shown by Du Rietz not to hold for lichen communities, except where very small areas are involved, and if we apply the formula to the phanerogamic population of the Channel Islands, which furnish a number of islands with a wide range of area, this formula is found to fail us again. The number of species on a given area is partly determined by the facilities for invasion, and is thus a function of the periphery of the selected area, but it is also greatly affected by the average size (area and height) of the component species. For a uniform habitat and a community of species where the individuals were all of approximately equal size, the number of species would probably show a relation to increasing area close enough to be approximated by a mathematical formula. But examining the data of even such uniform communities as the lichen communities studied by Du Rietz, we find that the number of species on a sq. metre ranges from three to eighteen; on a  $\frac{1}{4}$  sq. metre from two to fifteen and for 16 sq. metres from four to twenty-nine. Other examples could be cited showing similar differences, but with such deviations in a type of community that might be expected to yield relatively uniform results, the value of any pseudo-mathematical representation becomes highly problematical.

Hence it would seem undesirable to attempt any automatic system of regulating the size of the unit areas employed. It would, however, be desirable to adopt an arbitrary convention as to the size of the unit area to be utilised in the study of each well-defined physiognomic type. This arbitrary area could for example be large for phanerophytic synusiae whilst for some synusiae it could be small.

Reference may here be appropriately made to Palmgren's and Raunkiaer's "Law of Frequency." Importance has been attached by Raunkiaer and others to the fact that when species, in a homogeneous community, are classified in certain frequency classes there is a decrease in the percentage present in each class, in the order of increasing frequency, except the class of highest frequency, in which the percentage of species is higher than in the penultimate class. The fact that this is only applicable to homogeneous communities and



not to heterogeneous assemblages implies the presence of a certain proportion of species which are evenly distributed throughout and which are the basis of our judgment of homogeneity. The fact that the greatest number of species belong to the lowest frequency class is to be expected on the basis of probability, as also the general form of the falling curve, but the rise in the highest frequency class has been held to be important. This feature is, however, a necessary corollary of the manner of selection of quadrats in a homogeneous community, for the very fact that certain species are present in most, if not all, the quadrats, means less space available for others. The more evenly distributed the species the more it will suffer from space competition with the most frequent and abundant species, hence the mere fact that certain species are dominant necessarily involves a diminution in the other classes proportional to the frequency of their occurrence, so that the penultimate class will be low in comparison with the ultimate class. The fact that the rise in the class of greatest frequencies does not occur when the quadrats are taken from a heterogeneous community confirms this, as also the increased prominence of the highest frequency class when the number of species is small.

The Law of Frequency is, in fact, no more than a quasi-algebraical expression of the probability distribution, having regard to the necessary consequences of our basis of selection. In its graphic form of presentation it is, moreover, liable to be utilised as a means of comparison of one community with another without due regard to the many pitfalls which lie in wait for those who compare one frequency curve with another.

The fact that the number of constants increases with the size of the area utilised renders it desirable that the term constant should be given precision by reference to a conventional standard.

The concept of the minimal area cannot be given a very precise meaning and, though perhaps affording a convenient method of indicating differences in special cases, it is doubtful if it affords any additional information to that furnished by other data.

To summarise with respect to floristic composition it is suggested that abundance, frequency and constancy should be determined in relation to a standard number of areas of an arbitrarily fixed size. Where the number of individuals per unit area is small the standard number of areas should be multiplied and the results based on the average. It cannot, however, be too strongly urged that the results should only be expressed by arabic numerals when based on actual counts. The use of literal symbols as employed by British Ecologists has the merit of precluding their statistical treatment, but to emphasise the serial nature of estimates roman numerals might be employed without great risk of their misapplication.

The value of Braun-Blanquet's concept of characteristic species is high as a diagnostic phytosociological index, but its importance necessarily depends on the degree of exclusiveness of the species, and even more on its uniformity

of distribution. A characteristic species, even if strictly limited to a particular type of community, has but little phytosociological value when it is of purely local occurrence. Rolf Nordhagen has recently shown that, for the Sylene region of Norway, characteristic species with any marked degree of exclusiveness are almost entirely absent, and one is there forced to rely on the constant and dominant species for the characterisation of the communities of that area (R. Nordhagen, *Die Vegetation und Flora des Sylenegebietes*, Oslo, 1927). Exclusiveness is in reality a type of frequency in which we are dealing, not with occurrence in a limited number of sample areas, but with the occurrence of species in the community as a whole, in relation to its occurrence in communities of other types. It is a ratio concerned with extensive studies and as such is commonly not based on numerical data and, therefore, its expression by literal symbols or roman numerals is to be preferred to a representation by arabic numerals—a practice which is to be deprecated. It cannot be too strongly urged that such estimates should never be treated as statistical data.

Greater precision in the use of the term "exclusive" would be gained by its employment with reference to the proportion of occurrences (as expressed in percentages) in geographically separated examples of one community as compared with its occurrence in corresponding examples of another. In the case of continuous areas extending over large tracts of country, percentage occurrence on an equal number of areas separated by equal and arbitrarily fixed intervals (e.g. 2 kilometres) in the two types of community could be utilised as a basis for comparison. Except when exclusiveness is absolute, a condition which rarely obtains, it will seldom be of the same order with reference to more than one other type. The current method of assigning a degree of exclusiveness to a particular species in a community, is illogical, and, moreover, tends to obscure the real relations. The exclusiveness of a species in one type of vegetation must be separately determined in relation to each other type with which it is compared.

The degrees of dominance to a large extent find numerical expression in the determination of height and area of species considered in relation to physiognomy. Sociability is based on subjective judgment, and it is doubtful whether a numerical basis would yield results of greater practical value. The use of numerical symbols for non-numerical data is here again to be deprecated.

Finally one would urge that if numerical symbols be employed for non-numerical determinations roman numerals should be used, and it should always be pointed out that the data are not statistical.

#### ENVIRONMENTAL DATA.

Of the environmental factors it is generally admitted that data as to rainfall, temperature, humidity and evaporation, light intensities and, if possible, wind velocity, are desiderata. With respect to these, however, it is often not

practicable to obtain data over a sufficient period to warrant more than tentative conclusions and, in view of the marked character of climatic fluctuations and the known periodicity to which they are subject, it is doubtful whether any useful purpose is served by obtaining data of temperature and rainfall except where continuous and continued observation is possible. Evaporimeter records over even short periods are useful, especially as a means of comparison between degrees of exposure in various communities or their separate strata. Humidity data, unless continuous or recorded at frequent intervals, are apt to be very misleading, but the stomatal frequency to which reference has already been made can be utilised as an indirect means of integrating the water relations of the environment.

Wind velocity data are desirable, especially where exposure is severe, and where, apart from the indirect effect on humidity, these wind velocities are sufficient to have a direct mechanical influence.

Topographical data respecting aspect, slope and altitude are so clearly necessary as to need no emphasis.

Attention may be drawn to the need, especially marked in the case of climatic data, for an explicit statement as to whether they are applicable to the habitat as a whole or have only been determined for a partial habitat.

Respecting the soil its stratification should be determined with regard to organic content, carbonate content and/or exchangeable bases, and hydrogen-ion concentration. The stratification (soil profile) with respect to natural water content should be determined during the growing season and during the seasons of maximum and minimum moisture. Determinations after heavy rainfall are desirable as a means of ascertaining the efficiency of the precipitation in respect to the successive strata of root-systems.

Except in intensive studies little can be accomplished with respect to the biotic factors, apart from the seasonal succession, assimilatory periods, relative heights, and density of shade cast by the respective species, which belong more properly to the domain of physiognomy. In detailed studies the rate of sexual and vegetative increase is one of the most important features to be observed.

Data regarding the abundance of browsing animals such as deer, rabbits, field-mice, etc., are desirable, and the occurrence of earthworms and mollusca have considerable significance as indicators of the habitat conditions.

#### SUCCESIONAL DATA.

As we are here concerned with the description of communities rather than the relations between them, succession phenomena will only be of minor importance when but a single and relatively stable community is being described. But since all communities are dynamic and not static, the successional status is an essential part of their description. The phases of primary and

secondary successions should be distinguished and their ascertained or supposed relations clearly indicated. Their diagnosis and delimitation should correspond to that of the climax community, so that what has already been said applies to these also and no separate method of description need be adopted. It is, however, particularly desirable that writers should distinguish between the observed facts and the interpretations placed upon them. In but few instances can the actual phases, in time, of a succession be directly observed and the separation, as far as possible, of observation and interpretation will add both to the clarity and utility of such descriptions, whilst should the interpretation of the supposed succession ultimately require modification or even prove invalid, the recorded facts will still retain their full value. Furthermore, the mingling of facts and inference as to succession is very liable to result in the omission of data that the investigator has acquired which, though valuable in themselves, form no part of the evidence for the postulated succession.

The rôle of different species in the process of succession is very varied, some species accelerating, others retarding, the normal phases of development. Thus, on English salt-marshes, the early advent of *Obione portulacoides* may greatly retard or even apparently inhibit further development, whereas *Glyceria maritima*, which may appear very early in the succession or relatively late, greatly accelerates the process of development. As Prof. Rübel has suggested to me, it is desirable that the successional data should include mention of those species which have any such special significance, either as accelerators of succession or regression, or as stabilisers.

In the foregoing suggestions I have endeavoured to outline a basis upon which greater uniformity might be attained. It is most undesirable that any scheme of description should be generally adopted which is not sufficiently flexible to meet the needs of investigators with diverse points of view. But if such data as here indicated were included in every description of a plant community, it would render valid comparison possible between the observations of different workers whilst permitting that individuality of treatment which is equally essential to progress.

The author is indebted to various ecologists for the opportunity of discussing his views with them and, in particular, to Prof. Tansley for helpful criticisms in respect to the form of their presentation.

# A FURTHER CONTRIBUTION TO THE STUDY OF CYCLES IN BRITISH VOLES (*MICROTUS*)

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(With One Map.)

## I. INTRODUCTION.

IN a preliminary survey of the data concerning the fluctuations in numbers of British voles, written in November 1929 (Middleton, 1), it was shown that the maximum periods of abundance during the past 40 years fall into a more or less regular cycle of about 4 years. Methods were evolved for the purpose of obtaining more reliable evidence regarding future fluctuations, including an annual trapping census carried out on a number of areas in Great Britain, and a system of reports from observers throughout the country. In the present paper will be given the results of the past year's investigation correlated with and extending the previous work.

The research is being financed by the Empire Marketing Board, and is carried on under the direction of Mr Charles Elton in the Department of Zoology and Comparative Anatomy at Oxford, by kind permission of Prof. E. S. Goodrich, F.R.S. The writer wishes to thank the many observers throughout the country who have so readily given both information and practical assistance in the work. The Forestry Commission and many private estate owners have continued to give valuable facilities and arrange for trapping operations in many parts of the country.

## II. THE VOLE CENSUS.

The trapping census originated in 1929 was repeated in 1930 on the same areas, and a number of additional censuses were taken on new areas. The procedure adopted was practically the same as in 1929, 50 unbaited break-back traps being placed in runs in a line at about 5-yard intervals, and visits made every 24 hours; the position of the 1930 trapping line was not exactly the same as in 1929, but was moved 10 yards to one side of the previous line. The number of days trapping was reduced to five, in order to obviate the necessity for Sunday work on the part of foresters and others carrying out the census, and the period chosen was from August 11th to August 16th: except in one or two instances this period was strictly adhered to by the persons responsible for the trapping. The complete results of the trapping for both 1929 and 1930 are given in the table. In order to make a correct comparison between the two years, the results of 5 days' trapping only have been given



Table I. *Vole census results, 1929 and 1930. (5 days' trapping.)*

Place and County	Date	1929			Date	1930		
		Field voles	Wood mice	Shrews		Field voles	Wood mice	Shrews
Wilsey Down, Cornwall	Sept. 6	24	—	4	Aug. 11	5	—	2
Halwill, Devon	Sept. 5	10	—	1	"	6	2	3
Eggesford, Devon	Sept. 3	11	4	3	"	10	—	—
Haldon, Devon	Oct. 10	4	8	—	"	4	9	—
Wareham, Dorset	Sept. 9	—	—	3	"	—	—	1
Exmoor, Somerset	Sept. 11	4	1	2	"	3	11	5
Quantocks, Somerset	Sept. 19	4	7	1	"	4	11	3
New Forest, Hants.	Sept. 16	6	6	1	"	24	3	—
Dean Forest, Glos.	Aug. 21	6	3	—	"	26	4	3
Newcastleton, Roxburgh	Aug. 5	15	—	9	"	42	—	8
" " (2)	"	34	—	10	"	56	—	4
Lauder, Berwick	Aug. 1	55	—	14	"	28	1	6
Closeburn, Dumfries	"	13	1	6	"	13	1	6
Thornhill, Dumfries	"	4	—	2	"	12	1	2
Blairadam, Fife	Oct. 21	56	1	—	Aug. 16	34	1	—
Drummond Hill, Perth	Oct. 31	9	3	1	Aug. 11	34	1	6
Montreathmont, Angus	Oct. 14	5	2	—	"	2	—	—
Balmoral, Aberdeen	Oct. 8	35	3	—	"	7	—	—
Kirkhill, Aberdeen	Aug. 5	17	—	5	"	8	3	2
Huntly, Aberdeen*	"	45	—	16	"	16	—	9
Deer, Aberdeen	Aug. 1	14	—	22	"	13	—	3
Corrour, Inverness†	Nov. 8	10	6	1	Aug. 16	8	—	4
Glenmore, Inverness	Aug. 19	21	—	1	Aug. 11	15	—	1
Glenurquhart, Inverness	July 26	71	—	9	"	37	—	7
Glenhurich, Inverness	Nov. 27	78	—	—	"	4	—	3
Glenfinart, Argyll	Aug. 1	137	—	4	"	—	—	—
Teindland, Moray†	"	23	—	14	"	6	—	4
Lethen, Nairn	Aug. 6	71	—	6	"	20	4	3
Ratagan, W. Ross	Aug. 5	48	—	6	"	—	—	4
Ardross, E. Ross	Aug. 12	21	—	6	"	28	—	8
Loch Maree (Mainland)	Aug. 1	56	8	6	"	23	4	6
Loch Maree (Island)	"	12	—	8	"	3	—	1
Isle of Mull	Aug. 5	31	—	9	"	37	—	8

\* Heavy storms in August 1930 made traps inefficient.

† Area heavily poisoned in spring of 1930.

† Two days' trapping only, in 1929.

Table II. *Vole census results, one year only. (5 days' trapping.)*

Place	Date	1929			Bank voles
		Field voles	Wood mice	Shrews	
Beaulys, Inverness	Aug. 12	11	1	14	—
Lyminge, Kent*	Aug. 11	—	5	—	—
Chiddingfold, Surrey*	"	—	8	—	—
Nacton, Suffolk	Aug. 19	2	—	—	—
Thetford, Norfolk	Aug. 11	4	6	1	—
Finchampstead, Berks.	"	6	6	—	—
Brecon, S. Wales	"	11	—	9	—
Carmarthen, S. Wales	"	24	2	—	—
Dean Forest, Glos.* (2)	"	—	5	4	—
Corris, Mid-Wales	"	35	—	—	9
Beddgelert, N. Wales	"	10	10	9	5
Woodstock, Oxon. (A)	"	3	—	2	1
" " (B)	"	5	—	2	1
" " (C)	"	3	1	2	—
Walcot, Shropshire	"	8	—	—	—
Delamere, Cheshire	"	14	12	3	3
Cannock Chase, Staffs.	"	2	13	11	—
Clipstone, Notts.	"	—	5	—	—
Selby, Yorks.	"	8	—	3	—
Thornthwaite, Cumberland	"	40	2	1	1
Chopwell, Durham	Aug. 21	33	1	1	—
Rothbury, Northumberland	Aug. 11	12	23	9	—

\* Census carried out in woodlands instead of on grass area.



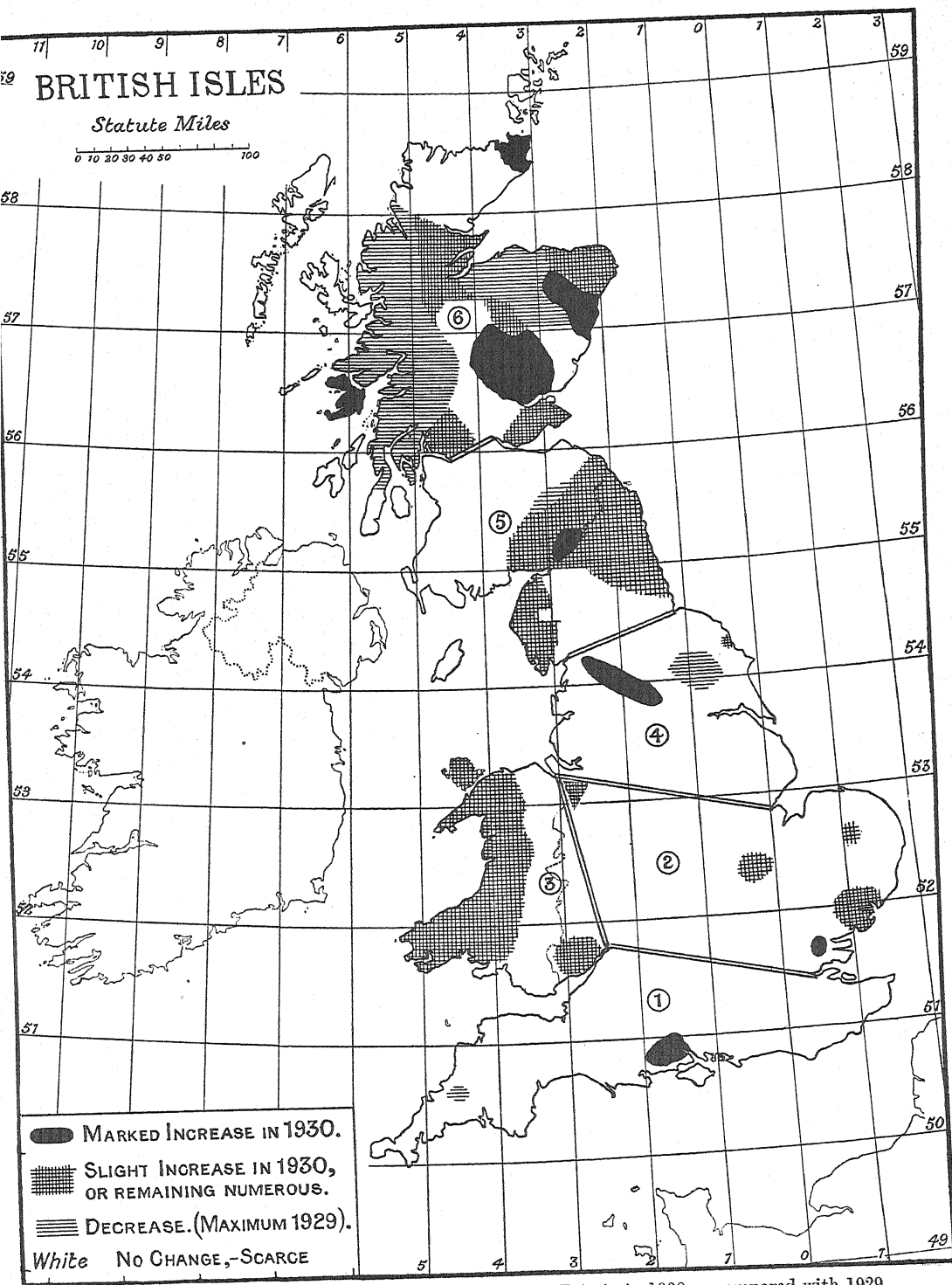
for the 1929 census, although in that year the census was actually carried on for 6 days. The results of this were given in the previous paper (Middleton, 1).

The working of this trapping census has in practice not been found very satisfactory, and it appears probable that the results are liable to a number of errors. Observations of vole-infested areas show that there is a considerable localised variation in the concentration on any one area, possibly arising from expansion of colonies or local migration. For example, during the vole plague in Argyll in the winter and spring, 1929-30, the distribution was by no means uniform, areas of several acres swarming with voles, while on other parts of exactly similar nature hardly a vole could be found; and in some parts of the area vole traces (droppings, runways, damage, etc.) were abundant, but few voles were actually on these spots at the time. A similar state of affairs existed in the Keswick region of Cumberland at the same time, where voles were very numerous but not uniformly distributed over the whole area. The effect of weather conditions on trapping in the exposed areas frequented by voles is also a source of considerable trouble, as it influences the efficiency of both the traps and the trapper, and probably the activity of the voles themselves. Other trapping experience in various parts of the country has shown that heavy rainfall has a pronounced effect on the results of trapping. The extreme variability in the weather conditions at various points between the south of England and the north of Scotland during a short-period census in August probably entails significant errors in results for comparison with each other and with previous censuses. The question of definitely reducing the population on census areas in cases where very few voles are present must also be considered. As it is impossible to make mathematical corrections for all these errors, and a really effective trapping census would entail more work than most voluntary trappers could be expected to do, it is proposed to reduce the number of censuses as carried on at present, and to evolve more accurate methods for application on a limited number of areas.

Striking instances of increase or reduction in numbers are, however, undoubtedly shown by the trapping censuses, but minor variations cannot be regarded as significant. The relative evidence regarding numbers given by competent observers appears to be a more satisfactory index of the fluctuations, and, although not statistical, enables more or less accurate maps of the population to be compiled. The map showing the position in the year ending September 30th, 1930, is compiled mainly from observational evidence. From many of the census areas additional observational evidence has been obtained, and this does not always agree with the results of the trapping.

### III. NUMBERS IN 1930.

The accompanying map, showing the vole population in 1930, has been divided into six arbitrary areas, and the position in each area will be discussed in detail as far as the reports available will allow. Reports from some



Map showing the changes in the vole population of Great Britain in 1930 as compared with 1929.

localities have not been received up to the time of writing, but it is thought that little information of importance is likely to be omitted from the following summary.

*Area 1. Southern England.*

One area only in the south of England shows any notable increase in numbers for 1930. In the New Forest region of Hampshire numbers have been considerably higher than usual (F. H. Haines, and result of vole census). The Cornwall, Devon, and Somerset censuses record low numbers of voles, although wood mice (*Apodemus*) appear to have increased in the Exmoor, Quantocks and Haldon areas. The yellow-necked wood mouse (*Apodemus flavicollis*) was found to be numerous in the Andover district of Hampshire in the autumn of 1930 (J. R. Groome). Continuous trapping which has been carried on at Wilsey Down, Cornwall, shows that voles were fairly numerous there in the autumn of 1929, but suffered a marked decrease in numbers in the spring of 1930 (J. Chrichton). In south-east Hampshire and the Isle of Wight nothing abnormal was noticed (A. Arnold). From north Hampshire (W. Balgarnie), south Berkshire (M. A. Carlisle-Crowe), Surrey (C. G. O. Bond; A. Beadell), Sussex (E. Aston; J. A. Harrison; C. Hazelman), Wiltshire (Miss Duncan), north Somerset (J. Furze), Dorset (W. Ford; the writer), and Kent (E. G. B. Meade-Waldo), reports indicate comparative scarcity or average numbers with no noticeable increase over 1929. From Cross-in-Hand district of Sussex a slight increase is recorded (H. W. Stone), and wood mice are numerous in the Edenbridge district of Kent (E. G. B. Meade-Waldo).

*Area 2. The Midlands and East Anglia.*

Throughout most of this area voles appear to have remained at rather a low level in 1929 and 1930. In north Northamptonshire they are reported as distinctly numerous in the summer and autumn of 1930 (J. W. Lee), but in south Northamptonshire no change was noticeable (the writer), and in the Rugby area of Warwickshire numbers are reported as normal (R. Campion). No change has been noticed in north Shropshire (H. E. Forrest) and south Shropshire (F. Pitt), but a slight increase is recorded in the Broseley district (G. Potts), and at Delamere in Cheshire the census indicates that voles are fairly numerous. Oxfordshire and north Berkshire appear to have shown little or no increase from the low numbers of 1928 and 1929 (the writer). In south Lincolnshire no change is recorded (T. C. P. Beasley), but in East Anglia marked increase is noted at Hickling, Norfolk (J. Vincent), and in east Suffolk (J. A. A. Forster; H. Drake), while "average" numbers are reported from the Merton district of Norfolk (F. Woolsey). Voles and mice were abundant in the Epping Forest area of Essex in the summer and autumn of 1930 (A. Hibbert-Ware), but in the Coggeshall district they are reported as scarce (A. R. Thompson).

*Area 3. Wales and Borders.*

In the Forest of Dean a considerable increase has taken place during the year, and numbers are now fairly high in some of the grasslands of that district. In the Brecon and Carmarthen districts of South Wales voles were fairly numerous in the autumn of 1930, but continuous observations have not been made on those areas. In the Corris Valley, mid-Wales, numbers have remained at a rather high level throughout 1929 and 1930, with little indication of increase or decrease (J. Lomas; F. C. Best), and the same applies to a considerable area in east Montgomeryshire and Cardiganshire (F. C. Best). In the Snowdon area of Caernarvonshire voles and mice have been numerous throughout 1930, but no pronounced increase seems to have taken place during the summer (J. Brown; the writer). In Anglesey an increase has occurred (S. Lloyd), though numbers are not high throughout the island (W. Mason).

*Area 4. The North Midlands and Yorkshire.*

Over a considerable area in the West Riding of Yorkshire voles appear to have become numerous in 1930; from the Settle district (A. E. Montagu), Keighley district (R. Butterfield), Airedale generally (F. H. Edmondson), and the district immediately south of Leeds (P. Baldwin), a noticeable increase is recorded. A limited area in the Hackness district near Scarborough, East Yorkshire, also shows an increase, but other localities in the same region remain with low numbers (W. J. Clarke). At Sleaford, Lincolnshire, wood mice have been numerous but voles normal (Sir G. Whichcote), while at Leadenham in the same county no change has been noticed (J. S. Reeve). In the York (S. Smith; W. Brown), Skelmanthorpe (F. Lawton) and Goathland (R. J. Flintoff) districts of Yorkshire numbers have been low, and similar conditions prevail in the Preston district, Lancashire (S. Crook), and North Nottinghamshire (T. Anderson).

*Area 5. Northern England and Southern Scotland.*

In the Border country many areas have shown a marked increase in numbers during 1930, although nothing approaching a plague is indicated at the moment. In the English Lake District increase is recorded for certain localities, as Windermere (E. J. Nurse), Keswick district (N. Laney; the writer), and the Crake Valley, near Ulverston (J. F. Musham), but low numbers are reported in the Ambleside (A. Astley), Cartmel (W. Coward), and Conistown (W. G. Wilson) districts. In the Alston district of Cumberland no change has been noticed (G. Bolam). In north Northumberland generally a slight increase has been noticed (J. G. G. Rea), and a more decided increase in the Wooler district (E. I. Grey; G. G. Rea). The census at Rothbury, Northumberland, shows a considerable number of voles, and a very high population of wood

mice for a grass area (C. Scott). In the Chopwell area of Durham voles are also distinctly numerous (W. Hodgson). At Chrichness, Berwickshire, an increase occurred (W. Caverhill), but at Mungoswalls in the same region no change was recorded (J. P. Ross-Taylor), and at Lauder the numbers remained at high level with little indication of increase (J. Lindsay). No change is reported on the Lammermoor Hills (A. R. MacDougall), Tweeddale, Peebles (M. G. Thorburn), nor in north Lanarkshire (M. G. Hamilton). In the district of Newcastleton, Roxburghshire, continuous trapping operations throughout the year and the double census on the forestry area show that voles are very much more numerous than in 1929 (J. F. Macintyre, etc.), and at Ancrum in the same county they are reported to have at least doubled their numbers during 1930 (A. J. Rintoul). In the area round Thornhill, Dumfriesshire, reports also show a marked increase in numbers (H. Gladstone) which is supported by the results of the census in that region (A. Menzies). On the hill pastures at the head of the Borthwick Valley, Selkirkshire, voles were very numerous in the autumn and winter, 1929-30, but were reduced to an absolute minimum in April and May 1930, and are now scarce in that area (A. Moffat).

#### *Area 6. The North of Scotland.*

In several areas in the northern half of Scotland 1929 was undoubtedly a maximum year for voles, and heavy reductions in numbers occurred during the spring and early summer of 1930. As noted in last year's report (Middleton, 1), voles were exceptionally numerous in the Cowal district of Argyll in the autumn of 1929, especially in the Glenfinart and Benmore district (round Loch Eck). In February 1930 a visit was made to this district by the writer and investigations carried out on the ground. Throughout the period August 1929 to March 1930 the numbers were very high, and by the end of February, on many parts of the forestry areas, the ground vegetation of grass, mosses, and rushes was so eaten down that it appeared unlikely that the heavy vole population would survive until the onset of spring growth in the plants produced a plentiful food supply. A great deal of damage was done throughout the winter to young trees in the plantations by ringing and nipping off branches of many species. Although voles were numerous throughout the whole district, trapping showed that the distribution was by no means uniform, even in identical conditions, and the voles appeared to have vacated many parts of the area where the eaten vegetation and damaged trees indicated their former presence in large numbers. Owing to adverse weather conditions it was difficult to carry out trapping operations which would give an accurate index of the numbers in particular localities. Trapping was carried on continuously in the young forestry plantations by the officials of the Forestry Commission, and part of the catch was examined by the writer. From February 18th to 21st 56 voles (*Microtus*), 5 wood mice (*Apodemus*), 7 common shrews (*Sorex araneus*), and 7 pigmy shrews (*Sorex minutus*), being a random sample of the



catch obtained in pit-fall traps, were examined: all the animals appeared to be in perfectly healthy condition, and the reproductive organs were in the normal winter condition, showing no signs of the onset of sexual activity. Of the 56 *Microtus* examined at this time 36 were males and 20 females. From March 15th to April 4th weekly samples of voles were examined, 66 in all, of which 39 were males and 27 females. After March 21st all the males examined had large testes and were apparently in breeding condition, but none of the females showed the slightest sign of copulation or sexual activity. It will be noted that the sex ratio indicated by these examinations was extremely high, being one of 160 males to 100 females. The only evidence of breeding voles in this district in the spring of 1930 consists of one nest with two young, found at Glenbranter (the northern part of the area concerned) on May 7th (J. Calder).

From the trapping operations and observations on the area, it appears that a considerable reduction in numbers occurred from the middle of March to the end of April: by the middle of June not a vole could be seen on the area (J. Fraser; H. MacMillan), and during the trapping census in August at Glenfinart not a single animal of any species was caught. (In the corresponding census in 1929 137 voles, 4 shrews and 27 bank voles were caught.)

During February and March 1930 dead voles were found occasionally on several parts of the area, and some of these were examined bacteriologically. No definite cause of death was ascertained but, as the voles had usually been dead for several days before examination, this is not surprising. Six voles were obtained alive from Glenfinart in February, and one of these died later in captivity at Oxford of a haemorrhagic septicaemia. A bacillus was isolated from this infection which appears to be similar in character to *Pasteurella muriscepticus* (C. S. Elton, unpublished work). Owing to the difficulty of getting any live voles from Argyll at this time it was impossible to carry out satisfactory bacteriological work in order to determine conclusively whether an epidemic disease was the cause of the marked reduction in numbers—as is strongly indicated by the circumstantial evidence.

Birds of prey were not noticeably abundant during this plague in Argyll, although they were stated to be more numerous than usual (J. Fraser). Weasels have been very numerous on the area during the summer of 1930, and have become more noticeable since the disappearance of the voles (H. MacMillan). A similar state of affairs existed in the same area in 1927 (Middleton, 1). It is interesting to note that bank voles, wood mice and shrews appear to have decreased on this area in a similar manner to the field voles, as they were certainly numerous at the time of vole abundance. No bank voles (*Evotomys glareolus*) were present among the voles and mice examined by the writer during February, March, and April, 1930, although they were evidently numerous at the time of the August census in 1929: it appears probable that the bank voles suffered a reduction before the other species.



Although a considerable amount of information was gained in the short time available regarding the effects of vole abundance in Argyll at this time, it is much regretted that facilities, monetary and otherwise, would not allow of a more thorough investigation being made of this extremely interesting plague. It is obvious that such an investigation would throw a great deal of light upon the whole question of cycles in numbers, and would be well worth the expenditure of time and money involved, but it may be pointed out that the same area experienced vole plagues in 1922-3, 1926-7 and 1929-30, so there seems good reason to suppose that the case summarised above will not be the last of the series.

Certain other areas in northern Scotland also experienced a maximum in 1929, notably western Ross-shire as shown by Ratagan (on the shores of Loch Duich) and the Loch Maree district. At Ratagan the numbers were very high in 1929, and amounted to a plague in the forestry plantations, but a reduction to an absolute minimum occurred in the spring of 1930, and no voles were caught in the census in August 1930 (W. Murray). At Loch Maree a considerable reduction from the abundance of 1929 has occurred, but voles are not so extremely scarce there as in the Argyll and Ratagan districts at the present time. In southern Inverness-shire a similar reduction has occurred at Glenhurich (W. Anderson), Corroul (S. Cameron) and Fort William (W. J. Cuthbert); in the northern part of the county the reduction does not appear to be so pronounced. At Glenurquhart in 1929 voles were very numerous, and are still numerous at the time of writing, although there has been no noticeable increase, and possibly a slight decrease (W. Macintosh; the writer). Similarly Glenmore in the Cairngorm district does not seem to have had any marked variation during the two years, though voles are fairly numerous (J. Kennedy); at Grantown-on-Spey they are reported as normal (G. Browne), and in the Nethybridge district no change from a normal scarcity has been observed for many years (W. Marshall). In east Ross-shire at Ardrross an increase is recorded and numbers are fairly high there (G. Anderson). On the island of Mull an increase has occurred, giving fairly high numbers for 1930 (J. Drysdale), but on Bute they are reported to be less in 1930 than 1929 (A. Smart). In Caithness a considerable increase is recorded (A. Sutherland). In Morayshire a decided drop in numbers has occurred from the very heavy population of 1929 (D. Paterson; A. Warren; F. Machray). In Aberdeenshire numbers have remained fairly high at Pitfour (A. Ross), increased considerably in the Huntly (J. Clark) and Bucksburn (F. L. Annand) districts, and decidedly decreased at Balmoral (J. Edwards). Further south, Montreathmont, Angus, records little change, with numbers rather low (J. McConnell), but in some parts of Fife an increase has taken place (A. J. Rintoul), and at Blairadam the high numbers of 1929 appear to have been maintained with perhaps a slight decrease (M. Macrae). The census shows a decided increase at Drummond Hill, Perthshire, in 1930, and reports from the Blair Atholl and Dunkeld districts of the

same county show voles to be unusually numerous (R. Inglis). On the south-eastern slopes of the Grampians throughout southern Forfarshire voles have shown a marked increase in 1930, and are very numerous in many localities at the present time (D. D. Volume). A considerable increase is also reported from west Stirlingshire (J. Bartholomew).

#### IV. THE VOLE CYCLE.

In view of the evidence obtained during the past two years it is obviously impossible to state that either 1929 or 1930 was a "mouse year" for the whole of Great Britain. It is quite certain that 1929 was a maximum year for several areas in Scotland, notably southern Argyllshire and western Ross-shire, as in these areas voles were at a pronounced peak in numbers in the autumn of 1929 and remained so during the following winter, suffering a remarkable reduction in the spring and early summer of 1930. Regarding the areas which experienced a maximum in 1930 it is impossible to give any conclusions until the 1931 populations have been studied, as a peak year can more readily be deduced from the sudden fall in numbers which follows it than from the actual numbers in the year concerned. The number of areas from which reports of increase have been received indicates that a more widespread occurrence of maxima is probable for 1930, although there are no areas at present with such high concentrations as that experienced by Glenfinart in 1929.

It seems that the comparatively regular cycle in numbers indicated by an examination of past records, described last year (Middleton, 1), is considerably modified by local conditions, and in some areas may actually have little or no influence on the voles and mice. It is possible that it is only in the presence of favourable local conditions that the cyclic influence becomes evident, while unfavourable conditions may permanently outweigh this influence in many districts, and in others the numbers may be kept below noticeable abundance in some "peak years." The fact that the dates of so few important maxima during the past 30 years disagree with this periodicity indicates that especially favourable local conditions are rarely powerful enough to produce a vole plague at a time when the cyclic influence is at a minimum, although they may stimulate increase sufficiently to bring about a maximum vole population in some areas in the year before the real peak of the general cyclic influence.

#### SUMMARY.

Further data are brought forward regarding the cyclic fluctuations in numbers of British voles (*Microtus*), mainly with reference to numbers in the years 1929 and 1930. In several parts of Great Britain 1929 was a maximum year and there is evidence that 1930 is probably a peak year in many other areas.

#### REFERENCE.

- (1) Middleton, A. D. "Cycles in the numbers of British Voles (*Microtus*).<sup>1</sup>" This JOURN. 18, 156-65, 1930.

## NOTICES OF PUBLICATIONS ON ANIMAL ECOLOGY

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*Note.* The objects and scope of this system of abstracts are explained in the *Journal of Ecology*, 16, p. 172 and p. 399, 1928.

### 1. GENERAL PAPERS ON PARTICULAR GROUPS OF ANIMALS.

**Witherby, H. F.** "New British Birds and Alterations to the British List." *British Birds*, 24, pp. 22-25. 1930.

Includes some changes in nomenclature.

**Harrison, J. M.** "Sight Records." *British Birds*, 23, pp. 342-344. 1930.

A letter raising the question of the validity of identifications of rare birds made by sight in the field. The editor gives in reply a very useful list of rules to guide observers in this matter.

**Richards, O. W.** "The British Species of Sphaeroceridae (Borboridae, Diptera)." *Proc. Zool. Soc. London*, pp. 261-345. 1930.

Contains a large number of important ecological notes upon habitats, enemies, food, etc., in addition to the main systematic account.

### 2. ECOLOGICAL SURVEYS AND HABITAT NOTES.

#### (a) MARINE.

**Colgan, N.** "The Marine Mollusca of the Shores and Shallow Waters of County Dublin." *Proc. Royal Irish Acad. Ser. B*, 39, pp. 391-424. 1930.

A list of species from various named stations, with a good deal of general habitat data.

**Heron-Allen, E.** "The Foraminifera of the Plymouth District. II." *Journ. Royal Micr. Soc.* 50, pp. 161-199. 1930.

Lists of species, with little ecological data.

#### (b) FRESHWATER.

See also Section 2 (c) (**Oldham, Peters**).

**Balfour-Browne, F.** "The Aquatic Coleoptera of the Mid-Ebudes." *Scottish Nat.* pp. 51-59. 1930.

Lists of water-beetles from Coll and Tiree, with comments (accompanied by maps) on the distribution of *Haliphus obliquus* and *Paracymus nigro-aeneus* in the British Isles.

**Shute, P. G.** "A Contribution to the Biology of *Taeniorhynchus richardii* (Dip.)." *Entomologist*, 63, pp. 133-136. 1930.

This mosquito was found in houses, etc., and the larvae attached to roots of water plants.

**Scott, A.** "Note on the Fauna of a Freshwater Pool on Bardsey Island."

*Proc. and Trans. Liverpool Biol. Soc.*, **43**, pp. 77-80. 1929.

Seventeen species of Crustacea and one *Volvox* are listed.

(c) LAND.

**Joy, H. N.** "Beetles in Birds' Nests." *British Birds*, **23**, p. 280. 1930.

An appeal to ornithologists to send birds' nests to Mr Joy (78, Crescent Road, Reading), who desires them collected and preserved in a special way which can be ascertained by writing to him.

**Robbins, J. C.** "A Dipterous Leaf-Miner in *Cephalanthera grandiflora*."

*London Nat. for* 1929, p. 76. 1930.

A fly, *Chylizosoma vittatum*, mining leaves of this orchid (the white helleborine) in Surrey.

**Foster, G.** "*Colletes daviesanus* at Bendeg, Co. Down." *Irish Nat. Journ.* **3**, p. 112. 1930.

Notes on a large nesting colony of this bee. Its parasite, *Epeolus*, does not occur in Ireland.

**Laidlaw, W. B. R.** "Notes on Some Humble Bees and Wasps in Scotland."

*Scottish Nat.* pp. 121-125. 1930.

Refers mainly to the Aberdeen district, but also to Mull and Edinburgh. Contains notes upon relative abundance of different species, seasonal activity, and species of plants visited.

**Laidlaw, W. B. R.** "New Locality for the Solitary Wasp, *Odynerus parietinus* Linn." *Scottish Nat.* p. 187. 1929.

This, the third record for Scotland, was from Direleton Castle, East Lothian, in August 1929. It occurred with *Bombus lapidarius*, *Psithyrus barbutellus* and *Vespa norvegica*.

**Stelfox, A. W.** "Maritime Species occurring Inland in County Wicklow."

*Irish Nat. Journ.* **3**, p. 83. 1930.

Two sandwasps (*Crabro peltarius* and *Tachysphex pectinipes*), a mason wasp (*Odynerus trimarginatus*), and a wolf spider (*Lycosa picta*) were found on an inland sandy area some 30 miles from the sea coast.

**Bristowe, W. S.** "The Spiders of Skomer Island." *Proc. Zool. Soc. London*, pp. 617-622. 1929.

Includes a general description of the island with a list of the spiders, with habitat notes (some from caves), and a record of spiders actually seen crossing the water between Skomer Island and the mainland on gossamer.

**Bristowe, W. S.** "The Distribution and Dispersal of Spiders." *Proc. Zool. Soc. London*, pp. 633-657. 1929.

An important discussion of these problems. *Pholcus phalangoides* (a species widely dispersed by man) has a distribution clearly correlated with temperature. A list of twenty other species with similar warm-climate distribution is given, together with a corresponding list of northern forms. The absence of certain species from islands is attributed partly to the effects of exposure and wind. It is pointed out that springtails, small flies, aphids, etc., are sometimes found entangled in spider gossamer, and may be dispersed in this manner.

**Bristowe, W. S.** "Notes on the Biology of Spiders: 3. Miscellaneous Notes."

*Ann. and Mag. of Nat. Hist.* Ser. 10, 6, pp. 347-353. 1930.

Includes notes on the habitats and distribution of two species of *Oonops*, several notes on the ecology of Indian spiders, and on spiders in birds' nests in Britain (rooks, gulls, shags, and cormorants).

**Womersley, H.** "Some Additions to the Collembola of Britain." *Ann. and*

*Mag. of Nat. Hist.* Ser. 10, 6, pp. 149-153. 1930.

Two of the species are from wasps' nests.

**Peters, B. G.** "A Biological Investigation of Sewage." *Journ. Helminthology*,

8, pp. 133-164. 1930.

Contains an account of the fauna found in and on sewage tanks and effluents (many Protozoa; also Nematodes, Rotifers, Gastrotricha, Worms, Crustacea, Flies, a Springtail, and a Tardigrade).

**Oldham, C.** "Notes on the Land and Freshwater Mollusca of Foula." *Scottish*

*Nat.* pp. 37-38. 1930.

Contains a few notes on habitats, and a list of species collected on this island of the Shetlands.

### 3. ANIMAL BEHAVIOUR AND THE ACTION OF ENVIRONMENTAL FACTORS.

SEE SECTION 7 ON NUMBERS OF ANIMALS.

**Graham, R. R.** "Safety Devices in the Wings of Birds." *British Birds*, 24,

pp. 2-21, 34-47, 58-65. 1930.

An important account of the mechanical arrangements of birds' wings, which are compared with similar devices upon aeroplanes. Birds have an equivalent to the slotted-wing of the Handley-Page aeroplane; also, in the bastard wing, a device resembling the Handley-Page auxiliary aerofoil.

**Jourdain, F. C. R.** "Green Woodpecker attacking Hives." *British Birds*, 23,

pp. 273-274. 1930.

Pecking holes in wooden bee-hives, but no evidence that the bees or honey were taken.

**Elliott, J. S.** "Starlings using a Roost in Summer." *British Birds*, 23,

p. 273. 1930.

Over 20,000 birds roosted in a chestnut plantation in June 1913, in Bedfordshire.

**Oldham, C.** "The Shell-Smashing Habit of Gulls." *Ibis*, 6, pp. 239-243. 1930.

Discussion of the significance of the habit, and as to whether it is instinctive or acquired in special circumstances.

**Wynne-Edwards, V. C.** "On the Waking-time of the Nightjar (*Caprimulgus*

*E. Europaeus*)." *Journ. Exp. Biol.* 7, pp. 241-247. 1930.

Contains evidence of a lunar periodicity in activity and breeding. It is suggested that this periodicity is controlled by variations in the effective length of night.

**Stelfox, A. W.** "Wasps' Nests: Their Normal and Some Unusual Situations."

*Irish Nat. Journ.* 3, pp. 98-101. 1930.

Records examples of a normally tree-nesting species of wasp (*Vespa sylvestris*) occupying underground sites (especially on wind-swept areas such as islands, but also in localities

with trees available), and of the normally ground-nesting species (*V. vulgaris*) occurring in a hedge on a summer-house. It is suggested that the wasps are more adaptable in habits than the usual ideas about their fixed instincts would indicate.

**Dunlop, G. A.** "Some Notes and Correspondence on a 'mixed' nest of *Vespa*." *North Western Nat.* 5, pp. 87-90. 1930.

An apparently mixed nest of *Vespa vulgaris* and *V. germanica*, which is discussed. A list is given of animals found in the nest (a fly, three beetles, a harvestman (Phalangid), and a centipede).

**Barnes, H. F.** "On the Biology of the Gall-Midges (Cecidomyiidae) attacking Meadow Foxtail Grass (*Alopecurus pratensis*), including the Description of One New Species." *Ann. Appl. Biol.* 17, pp. 339-366. 1930.

The high percentage of foxtail grass seed destroyed by insect larvae is a problem of some economic significance. The author found three species of midges were concerned: *Dasyneura alopecuri*, *Stenodiplosis geniculati*, and *Contarinia merceri* (new species), the last being the most important. The distribution and life-cycles of the species are described. A simple method of control is suggested: keeping sheep on the grass until after most of the midges have emerged, and thus delaying flowering of the grass until few midges remain to breed. In this way smaller heads of seed are obtained, but the higher percentage of ripe seeds compensates fully for this loss.

**Barnes, H. F.** "On Some Factors Governing the Emergence of Gall Midges (Cecidomyiidae: Diptera)." *Proc. Zool. Soc. London*, pp. 381-393. 1930.

The periodicity in times of emergence is very marked, and is correlated with certain environmental rhythms. The effects of this periodicity upon infestation of the midges by parasites is discussed.

**Wardle, R. A.** "Significant Variables in the Blowfly Environment." *Annals of Applied Biology*, 17, pp. 554-574. 1930.

An attempt to find a mathematical formula to fit the rate of increase of *Lucilia sericata* in respect to different conditions of temperature, humidity, etc.

**Bristowe, W. S.** "Notes on the Biology of Spiders: 1. The Evolution of Spiders' Snares." *Ann. and Mag. of Nat. Hist.* Ser. 10, 6, pp. 334-342. 1930.

**Bristowe, W. S.** "Notes on the Biology of Spiders: 2. Aquatic Spiders." *Ann. and Mag. of Nat. Hist.* Ser. 10, 6, pp. 343-347. 1930.

**Triffitt, M. J.** "On the Bionomics of *Heteroderes schachtii* on Potatoes, with Special Reference to the Influence of Mustard on the Escape of the Larvae from the Cysts." *Journ. Helminthology*, 8, pp. 19-48. 1930.

The author found by experiment that the roots of potatoes give off a substance which stimulates emergence of this nematode from its cysts. This substance is only given off while the plant is growing. It is fairly stable under sterile conditions (though not in unsterile conditions), and acts in minute quantities. Mustard roots give off another substance which inhibits the formation of cysts, and may therefore be of great importance in the control of the nematode pest.



## 4. PARASITES OF ANIMALS.

**Scott, A.** "The Copepod Parasites of Irish Sea Fishes." *Proc. and Trans. Liverpool Biol. Soc.* **43**, pp. 81-119. 1929.

A long list of species and their hosts, with notes on structure and life histories.

**Goodey, T.** "On the Nematode Parasite of the Frit-Fly *Oscinella frit*, L." *Journ. Helminthology*, **8**, pp. 123-132. 1903.

This species causes parasitic castration of the fly (which is an important pest of cereals).

## 5. PLANT GALLS.

See also Section 3 (**Barnes**).

**Burkill, H. J.** "A Contribution towards a List of the Plant Galls of Shropshire." *North Western Nat.* **5**, pp. 25-35.

A long list of species and their hosts.

**Burkill, H. J.** "Some Notes on Midge Galls 1929." *Entomologist*, **63**, pp. 59-61. 1930.

Gives hosts and species of midges, from various localities.

**Burkill, H. J.** "Plant Galls." *London Nat. for* 1929, pp. 107-111. 1930.

Many records of galls caused by different organisms.

**Burkill, H. J.** "British Gall Mites." *London Nat. for* 1929, pp. 58-68. 1930.

A complete list of the mites, with names of host plants, and references to the various records.

**Heslop Harrison, J. W.** "Two New Eriophyid Mites." *Proc. Univ. of Durham Phil. Soc.* **8**, pp. 168-170. 1930.

One species was forming galls on *Eryngium Bourgati* in the French Pyrenees, the other on *Thalictrum dunense* near Durham.

**Massee, A. M.** "A New Subspecies of Eriophyid Mite on Plum Galls." *Ann. and Mag. of Nat. Hist.* Ser. 10, **6**, pp. 145-148. 1930.

## 6. FOOD HABITS.

See also Section 7 (**Ritchie**).

**Brown, R. H.** "The Food of Certain Birds of Prey." *British Birds*, **23**, pp. 269-272. 1930.

A very important list of first-hand observations made in Cumberland and Westmorland. The birds include raven, owls, peregrine falcon (many observations), merlin, kestrel, buzzard, sparrowhawk, and heron.

**Davis, H. H.** "Food of Tawny Owl." *British Birds*, **24**, p. 24. 1930.

Remains of a moorhen, and of a green woodpecker found in a nest near Bristol.

**Patten, C. J.** "The Little Owl and Little Rabbits." *Irish Nat. Journ.* **3**, pp. 92-94. 1930.

Contains evidence that the little owl sometimes takes young rabbits.

**Allen, G. S.** "Diet of Young Buzzard." *British Birds*, **24**, p. 79. 1930.

A young buzzard in Pembrokeshire was fed by its parents during 19 days, upon thirty-nine rabbits, twenty-four moles, one weasel, three mice, two moorhens, five pheasants, one chicken, and one blackbird.

- Astley, A.** "Pied Flycatcher eating Worms." *British Birds*, **24**, p. 52. 1930.
- Brown, R. H.** "Pied Flycatcher eating Worms." *British Birds*, **24**, p. 76. 1930.
- Garnett, R. M.** "Little Gull feeding on Earthworms." *British Birds*, **23**, pp. 278-279. 1930.

**Moffat, C. B.** "Titmice eating Corn." *Irish Nat. Journ.* **3**, p. 90. 1930.  
Tits eating oats.

**Loewenthal, A.** "Blue Tits and Corn." *Irish Nat. Journ.* **3**, p. 55. 1930.  
Confirms the fact that they will eat corn.

**Davies, W. M.** "Notes on the Contents of the Crops of Wood Pigeons." *North Western Nat.* **5**, pp. 92-95. 1930.

Fourteen pigeons examined in February 1930, contained mainly ivyberries and leaves of *Ranunculus bulbosus* and *R. ficaria*, together with lesser amounts of leaves of *Trifolium repens*, *Rumex acetosa*, and grass. The author points out that this investigation, though limited in extent, does not confirm the theory of farmers that the pigeons damage clover, etc.

**Theobald, F. V.** "Notes on Insects Feeding on Hops in 1928 and 1929." *Entomologist*, **63**, pp. 7-10. 1930.

#### 7. THE NUMBERS OF ANIMALS.

See also Section 3 (**Wardle**); Section 8 (**Ritchie**).

**Baker, J. R.** "The Breeding-Season in British Wild Mice." *Proc. Zool. Soc. London*, pp. 113-126. 1930.

It is shown that the factors controlling the annual breeding rhythm in *Apodemus sylvaticus* and *Evotomys glareolus* are very little understood, and that there are important variations in the extent of breeding activity in different winters.

**Ritchie, J.** "St Kilda and the Significance of some of its Animal Inhabitants." *Scottish Nat.* pp. 69-74. 1930.

Contains chiefly a discussion of the position, past and future, of the fulmar petrel, an important food item of the islanders, and brings forward evidence to show that the recent spread and increase in numbers of this bird was due partly to the decreasing population of St Kilda, and partly to the change from natural to artificial foods accompanying the visits of mainland steamers since 1877.

**Tucker, B. W.** (edited by). "Report of the Oxford Ornithological Society and the Ornithological Section of the Ashmolean Society for 1929." *Proc. and Rept. Ashmolean Nat. Hist. Soc. of Oxfordshire for 1929*, Supplement, pp. 1-38. 1930.

Contains a number of notes on migration, changes in numbers, etc. Particular mention may be made of notes on effects of the cold spell in early 1929 upon bird life, many birds being killed, disappearance of house martin as a breeding bird, and immigration of crossbills.

**Riviere, B. B.** "Ornithological Report for Norfolk for 1929." *British Birds*, **23**, pp. 282-288. 1930.

Comments on effects of the cold spell early in 1929. Aquatic birds (herons, moorhens, waders, etc.) and also small land birds (thrushes, bearded tits, etc.) were killed. On the other hand it was an unusually favourable spring for the breeding of partridges and wild pheasants. Immigration of crossbills.



**Salter, J. H.** "Changes in a Local Avifauna." *North Western Nat.* 5, pp. 14-17. 1930.

Refers to the Aberystwyth district during a period of about forty years. Points dealt with are the destruction of small birds by the frost of February 1929, effects of dry and wet summers on the numbers of migrants, etc.

**Bond, W. R.** "Some Effects of a Cold Winter on Birds, and Other Observations." *Proc. Dorset Nat. Hist. and Arch. Soc.* 51, pp. 223-231. 1930.

Refers especially to the effects of the cold spell in February 1929, which killed many species of birds. There is also a note upon mortality among eels during cold winters in the Crimean War and in 1880, but not in 1929. The eel mortality was supposed to be due to snow water entering the sea in large amounts.

**Watson, J. B.** "Mortality amongst Swifts caused by Cold." *British Birds*, 24, p. 107. 1930.

Mortality on the Suffolk coast caused by heavy summer storms during the southward migration.

**Eggeling, W. J.** "Storms and Destruction of Bird Life." *Scottish Nat.* p. 8. 1930.

Sixty-five seabirds of various species found dead along a 2½ mile stretch of shore, after winter storms.

**Stewart, W.** "The Rook in Lanarkshire in 1922-29." *Scottish Nat.* pp. 15-21. 1930.

An important series of census statistics, repeating in 1929 the work done in 1922. It is estimated that the population had increased from about 18,800 in 1922 to 23,800 in 1929, but that this increase was mainly confined to an area in the east of the county equal to about 5 per cent. of the total area. In this region tremendous increase and colonisation of coniferous woods had occurred, and was causing annoyance.

**Inkster, C. J.** "House Sparrows return to Mid-Yell." *Scottish Nat.* p. 68. 1930.

Still very few sparrows on Mid-Yell (Shetlands), after epidemic in 1928 which completely wiped out all birds on the mid-part of the island, though not at the north and south ends.

**Duncan, A. B.** "A Bird Count in Lewis." *Scottish Nat.* p. 177. 1929.

A rough transect census from a motor car on different types of ground in 1929.

**M'Conachie, W.** "The Return of the Goldfinch." *History of Berwickshire Nat. Club.* 27, Part I, pp. 111-114. 1929.

The goldfinch was fairly abundant in the Berwick area in the early nineteenth century, but became very scarce by the middle of the century (also in other parts of Britain). At the end of the last century it began to reappear, and there has been a very marked increase from 1925 onwards, also in other districts on the border. The recovery is attributed to the laws prohibiting trapping of small birds.

**Corlett, G.** "The Winter Status of the Bass Rock Gannets." *British Birds*, 24, p. 53. 1930.

Notes made while on a destroyer between the years 1912 and 1918, raising the question of where the Bass Rock gannets go in winter.

**Rintoul, L. J. and Baxter, E. V.** "Bird Notes from Skye." *Scottish Nat.* pp. 85-87. 1930.

Includes many notes on changes in numbers and distribution.

**Lumby, J. R. and Atkinson, G. T.** "On Unusual Mortality amongst Fish during March and April 1929, in the North Sea." *Journ. du Conseil*, **4**, Dec. 1929 (reviewed in the *Scottish Naturalist*).

Contains a number of examples of mortality among marine fish, e.g. tile-fish off Newfoundland in 1882, cod off Labrador in 1876, haddock off Lapland and Norway in 1789, and soles, brill, cod, dab, plaice, and crabs, in the southern part of the North Sea in 1929. Most of these deaths are attributed to invasion of regions by unusually cold water.

**Storror, B.** "Cullercoats Herring Investigations and their relation to Other Marine Work: an Essay on Fluctuations." *Proc. Univ. of Durham Phil. Soc.* **8**, pp. 191-238. 1930.

Preliminary investigations showed that "a parochial point of view, such as would be obtained from the examination of local shoals only, was of little use for any understanding of the herring fishery." In the investigation of the problem of fluctuations "which is the greatest of all problems connected with fisheries," over 60,000 herrings were examined between 1919 and 1929. Starting with the idea that fluctuations depend "on the hatching, dying, and swimming of the fish," the author follows up each factor that may influence these processes, and is led to extremely interesting conclusions about the effects upon plankton and upon fisheries of the invasion of Atlantic water periodically into the North Sea. This paper opens up very effectively the large vista of work required for a proper understanding of fluctuations in fish numbers.

**Smith, W. C.** "A Study of the Manx Herring Shoals during the Period 1923-1928." *Proc. and Trans. Liverpool Biol. Soc.* **43**, pp. 17-76. 1929.

An extensive investigation, with many tables and diagrams, and discussion of variation in growth and age classes.

**Thompson, W. R.** "The Principles of Biological Control." *Ann. App. Biol.* **17**, pp. 306-338. 1930.

A general survey of the present prospects of biological control of insect pests. The author believes that epidemics, although occurring naturally to a certain extent, have not yet proved of any aid in artificial control, although experiments are being made in America with Mermithid Nematodes against grasshopper outbreaks; that vertebrate predators are seldom important in controlling insect outbreaks; but that insect parasites (Diptera, Hymenoptera, etc.) are yielding very promising and important results. The various factors involved in application of control of the last type are discussed, and some mathematical considerations introduced.

**Curtis, W. P.** "*Hyloicus pinastri* L. as a British Species." *Entomologist*, **63**, pp. 1-6. 1930.

Gives evidence that this moth is an endemic species which sometimes (as in 1929) has seasons of unusual abundance.

## 8. MIGRATION AND DISPERSAL.

See also Section 2 (c) (**Bristowe**); Section 7 (**Tucker, Riviere, Salter, Storror, Smith**).

**MacRae, J. E.** "The Grey Squirrel in Forfar." *Scottish Nat.* p. 164. 1929.  
Seen in August 1929.

**Ritchie, J.** "The Spread of the Mountain Hare in the Scottish Lowlands and Border Country." *Scottish Nat.* pp. 169-175. 1929.

The mountain hare was originally introduced into the Lowlands from the Highlands, during the years 1834-1868. It has gradually spread southwards and eastwards, and now lives on the Cheviots.

**Bedford, M.** "Increase of the Mountain Hare at Cairnsmore, Kirkeudbrightshire." *Scottish Nat.* p. 68. 1930.

**Saxby, T. E., Greenaway, W. H. and McDougall, W. L.** "Immigration of Northern Great Spotted Woodpecker to the Shetland Isles." *Scottish Nat.* p. 138. 1929.

A fairly extensive invasion in the summer of 1929. A further confirmation of these observations is made by **Bowie, J. C.** in *Scottish Nat.* p. 180. 1929.

**Holder, F. W. and Wagstaffe, W.** "The Migrations of the Bar-tailed Godwit as observed on the South Lancashire Coast." *British Birds*, **23**, pp. 318-323. 1930.

**Ritchie, J.** "Northward Extension of Capercaillie in Scotland." *Scottish Nat.* p. 176. 1929.

**Reid, D. N.** "Spread of Capercaillie in Ross-shire." *Scottish Nat.* p. 26. 1930.

**Various Observers.** "Invasion of Crossbills from the Continent." *Scottish Nat.* pp. 109-110. 1930.

**Witherby, H. F.** "Immigration of Crossbills." *British Birds*, **23**, p. 227. 1930.

**Witherby, H. F.** "A Plan for Simultaneous International Observation of Migration round the North Sea." *British Birds*, **23**, p. 338. 1930.

A scheme started by the new migration and ringing journal, *Der Vogelzug*, the idea being to obtain "synoptic charts" of the migration situation, analogous to weather charts, or to the wild duck migration maps compiled by the U.S. Bureau of Biological Survey.

**Frohawke, F. W.** "Comma in Surrey." *Entomologist*, **63**, p. 86. 1930.

Other notes by various writers on the spread of the Comma Butterfly (*Polygonia c-album*) during recent years are contained in the following references: *The Entomologist*, **5**, pp. 10, 58, 112, 115, 137, 138, 140. 1930. *London Nat.* for 1929, pp. 39-41. *North Western Nat.* **5**, pp. 39-40, 111. 1930.

Notes upon changes in numbers, and migration of various other butterflies and moths are also included in the following: *The Entomologist*, **5**, pp. 10, 40-41, 59-61, 112. 1930. *London Nat.* for 1929, pp. 39-41, 42, 85. 1930.

**Fisher, N.** "*Planorbis corneus* (Linn.) in County Antrim." *Irish Nat. Journ.* **3**, pp. 90-91. 1930.

This is a rare species in Ireland, and was possibly introduced by man.

**Welch, R. J.** "Foreign *Physa*, Ards, County Down." *Irish Nat. Journ.* **3**, p. 91. 1930.

An introduced American species, probably on garden water plants.

**Kevan, D. K.** "New Scottish County Records of Land and Freshwater Mollusca." *Scottish Nat.* pp. 27-29. 1930.

Includes notes on the recent extension of range of *Paludestrina jenkinsi*, which is still spreading in Scotland.

## *OBITUARY NOTICE*

CHARLES EDWARD MOSS.

THE premature and unexpected death, on November 11th, 1930, of Prof. C. E. Moss, at his home in Johannesburg, from haemorrhage of the lungs, has come as a great shock to his friends. He was on the point of sailing for England on leave, to continue at Kew and the British Museum his extensive work on the South African flora.



CHARLES EDWARD MOSS. 1870-1930.

Charles Edward Moss was born on February 7th, 1870, at Newton, near Dukinfield in North Cheshire, the son of a Nonconformist minister and the youngest of a family of six. In the same year his father, Benjamin, went with his family to Monk's Eleigh in Suffolk, but returned to the north four years later, settling at Halifax. It was here that Moss spent his boyhood,



getting his early education at Queen's Road Board School, and afterwards at Akroyd Place School, where he became a pupil-teacher, and at Parkinson Lane School.

As a young man Moss early showed a love for plants, and in 1892 he joined the botanical section of the Halifax Scientific Society. In the following year he developed a pulmonary abscess, necessitating an operation, and during his long convalescence was advised to be in the open air as much as possible. During this time he used to wander a good deal by himself with a vasculum and to join the rambles of the Yorkshire Naturalists' Union, becoming close friends with several local naturalists. By these means he made himself a competent field botanist, and it was this period of his life that evidently determined his later career.

After he had regained his health in 1895 he went, as a Queen's Scholar, to the Yorkshire College, Leeds, at that time one of the constituent colleges of the old Victoria University. Here he took his Teacher's Certificate, and in 1898, the degree of B.Sc. The late Prof. L. C. Miall, well known for his devotion to the "heuristic" method of teaching, was then Professor of Biology at Leeds, and his methods and general outlook were such as to appeal strongly to Moss's independent mind. Dr J. Welton, too, who was Lecturer in Education and Master of Method (later Professor of Education) and an inspiring teacher, became Moss's friend and greatly influenced the development of his naturally strong logical faculty. Moss contributed a chapter on "the Teaching of Nature Study" to Welton's *Principles of Education*.

In 1896 the late Dr W. G. Smith came to Leeds from Edinburgh, to be Miall's assistant in botany. Smith was full of the new work on plant associations recently begun by his brother Robert in Scotland (Robert Smith's *Plant Associations of the Tay Basin* was published in 1898), and determined to apply the method to the Yorkshire country. In Moss he found a willing pupil, and with his good knowledge of field botany, the foundations of which had been laid in earlier years at Halifax, an able collaborator. The first result was the publication in 1903, in the *Geographical Journal*, of a memoir on "The Geographical Distribution of Vegetation in Yorkshire (Leeds and Halifax District)," illustrated by a coloured vegetation map, by Smith and Moss, the first English "primary survey" memoir to appear. The eventual result was the important part played by Moss in the early development of the modern study of plant ecology in England. The work with Smith was by no means Moss's first publication. In 1896 he had published "Why do Flowers bloom in Spring and in Autumn?" in the *Halifax Naturalist*, recently started by his great friend Mr W. B. Crump. This was followed by papers "On the Structure of Crocus Leaves" (1899), "The Life History of the Autumn Crocus (*C. nudiflorus* Sm.)" (1900), and "The Moors of South-west Yorkshire" (1902), and by two papers in *The Naturalist* (the organ of the Yorkshire Naturalists' Union) on "Changes in the Halifax flora" (1900 and 1901).

The following extract from an appreciation (which appeared in the *Yorkshire Post*) by Mr W. B. Crump, gives a life-like picture of Moss as he appeared in the field at this time, and later also, at Cambridge. Moss's "keenness of vision and perception was accompanied by a nonchalance in manner that was quite deceptive. With his walking-stick in his hand, a big vasculum on his back and a roll of Ordnance maps under his arm, he sauntered along with an air of seeming indifference, at any rate until he reached a spot which he felt intuitively would repay a careful search. There he scanned every inch of a rock face, or a hedge bottom, or a scree slope, and he could detect even the small things at a distance. But though the vasculum was big, as often as not it was brought home empty. Moss was not a collector." But later, at Cambridge, when he had turned to the study of critical genera and species, "his vasculum" (which became larger and larger as time went on!) "was soon full if he went on a collecting expedition for such, especially if they were elms, oaks, birches or poplars...."

After graduating Moss taught for a while at Fairweather Green School, Bradford, and in January 1901 obtained a position as master at Sexey's School, Bruton, Somerset. Here he taught mainly botany, assisting in other subjects with the junior forms. His headmaster testifies that his work was excellent, and that the reputation of the school in botany was largely due to Moss's efficient teaching. This was his first introduction to the south English landscape and southern English vegetation, and he used his opportunities to the full. His paper on the "Geographical Distribution of the Vegetation of Somerset (Bath and Bridgwater District)" was published by the Royal Geographical Society in 1907, and the treatment, together with the accompanying vegetation map, marked a great advance on the earlier primary surveys. In December 1902 he left Somerset and, at some financial sacrifice, for he was anxious to abandon schoolmastering and to devote himself entirely to botany, went to the Municipal Training College at Manchester as Lecturer in Biology. He improved his knowledge of general botany by attending many of the Honours lectures at the Botanical Department of the University and took the M.Sc. degree, largely on the strength of his Somerset work. At this time also he began a vegetation survey of north Derbyshire, which afterwards won him the degree of D.Sc. This was not published till 1913, by the Cambridge University Press, in a handsome volume under the title of *Vegetation of the Peak District*, accompanied by two coloured vegetation maps, and with the aid of subsidies from the Royal Society and the Royal Geographical Society.

While Moss was at Manchester, the Central Committee for the Survey and Study of British Vegetation (afterwards known as the British Vegetation Committee, and the precursor of the British Ecological Society) was founded in December 1904, by the small band of botanists actively interested in the new method of work. From this date until Moss's departure for South Africa in 1917 the present writer's intimacy with him was close and continuous.

From the first, on account of his excellent and increasingly critical knowledge of field botany and of his continuous hard work and devotion to the subject, Moss was one of the most active and valuable members of the Committee, all of whom were exceptionally keen and enthusiastic. It was Moss who in his Somerset paper worked out precise concepts of the plant association and the plant formation, conceptions which were more fully elaborated in his "Fundamental Units of Vegetation" (*New Phytologist*, 1910) and made the basis of the treatment adopted in *Types of British Vegetation* (1911), a book to which Moss contributed largely and which could not have been written without his constant and loyal assistance.

During his later years at Manchester Moss became increasingly anxious for an academic and purely botanical appointment, and in 1907 he was invited by Prof. Seward to come to Cambridge as Curator of the University Herbarium. This offer he accepted and on arriving in Cambridge in January 1908 he joined Emmanuel College as a Research Student, taking his B.A. degree by research in due course. During his tenure of the curatorship at Cambridge he lectured on systematic botany, demonstrated to the elementary students, and was above all active in the field, where he was always an inspiring influence. During the earlier part of this period he remained an active member of the British Vegetation Committee, and took the main share in drawing up an elaborate scheme for the uniform colouring of vegetation maps, which, however, came to nothing, largely owing to the financial difficulty of publishing a continuous series of such maps. Moss always strongly held that vegetation survey of this country should be recognised by Government equally with geological survey. A scheme of subsidy of the maps was actually prepared in collaboration with the Ordnance Survey Office and supported by the Board of Agriculture, but the Treasury intervened at the last moment and disallowed the necessary grant. In 1910 he contributed the article on Plant Ecology to the eleventh edition of the *Encyclopaedia Britannica*.

From about this time Moss turned his attention more and more to floristic work. In 1910 he had contributed an illuminating article on "British Oaks" to the *Journal of Botany*, and this was later followed by one on "British Elms" in the *Gardener's Chronicle*, by a systematic revision of "Some species of *Salicornia*" in the *Journal of Botany* (1911), and by other smaller taxonomic contributions. All of these works showed critical insight combined with broad and sane views of the values of taxonomic units. About this time he conceived the idea of a monumental British Flora, illustrated by reproductions of a beautiful series of pencil drawings of British plants which had been executed by Mr E. W. Hunnybun of Huntingdon. His scheme was accepted by the University Press, which agreed to publish the work as *The Cambridge British Flora* in a series of folio volumes arranged according to the Englerian system. Moss was to edit the work and to write a large part himself. Certain genera he delegated to various specialists. The first volume (vol. II of the series)

appeared in 1913, and contained the Amentiferae and allied families, to which Moss had given special attention. This volume contains by far the best existing account of these plants. The outbreak of war, however, seriously compromised the financial chances of this ambitious undertaking, and in the event only one other volume (vol. III) was published after Moss's departure for South Africa, and was edited by Mr A. J. Wilmott of the British Museum, who had been one of Moss's pupils at Cambridge. The failure to complete *The Cambridge British Flora* is a very serious loss to our knowledge of British plants.

During the war domestic troubles seriously overshadowed Moss's life and in 1917 he accepted the appointment of Professor of Botany in Johannesburg at the University of the Witwatersrand. Here he set to work with great success both to build up his department and to acquire a knowledge of the flora of South Africa. His department he made a living centre of research—mainly floristic. His publications during the thirteen years he was in South Africa were limited in number, because with his accustomed thoroughness he would not publish until he had made every possible investigation and convinced himself of the truth of his conclusions by patient observation and comparison. He found grave inaccuracies and many wrong identifications in both published and herbarium material, and he constantly travelled widely throughout the Union, and far outside its limits, in order to see for himself in their native habitats the plants he was studying. He came to England several times in order to work at Kew and the British Museum, and he was on the point of starting on another of these visits, which was to have put the final touches to much of the work he had in hand, when he was overtaken by death.

Moss's death, indeed, has come at a most unfortunate time for his scientific reputation as an original investigator in the field of systematic botany. In a very few years more he would almost certainly have published a large body of work which would have securely established his reputation in this field of the science. He was at one time a candidate for Fellowship of the Royal Society, but his name was allowed to lapse because it was generally felt that the amount of his published work was as yet insufficient to justify botanists in pressing for his selection at that time. Of the quality of his work no one who knew it intimately had any doubt.

Moss combined a naturally acute and logical mind with keen love for his subject and great powers of work. He really made two reputations: the first as a pioneer in the development of ecology in this country, and one who contributed valuable guiding ideas as well as a great bulk of accurate field work: the second as a thorough and critical taxonomic worker who was never content with herbarium knowledge alone but always insisted on first-hand acquaintance in the field with the plants he was studying. Owing to the unavoidable disappointment over *The Cambridge British Flora* and to his untimely death the great results that should have accrued have not been realised during his life-

time, though it is hoped that much of his South African work is in a sufficiently advanced state of preparation to be completed by other hands.

It was not everyone that found Moss easy to get on with. He was incapable of putting himself in the position of anyone whose views differed widely from his own, and too apt to dismiss them with sweeping contempt. A little stiff and reserved in bearing he was withal very sensitive, and he had a certain reluctance to make allowances for the weaknesses of his fellows. He did not suffer fools gladly and he was given to expressing his disapprobation in language which was not intended to be offensive, but by its combination of precision and rather ponderous emphasis did in fact inflict wounds. He once said, rather ruefully, that he was sometimes accused of being waspish and sometimes of being elephantine; he hoped he wasn't either and at least he couldn't well be both! Nevertheless there were grains of truth in both accusations, and he never really learned how much he was apt to wound and irritate people. But he was not in the least malicious and he was a loyal and affectionate friend.

Moss was twice married and leaves a daughter by his first, and a son by his second wife, who was a member of his staff at Johannesburg and an invaluable coadjutor in all his later work.

A. G. T.

## REVIEWS

Ridley, H. N. *The Dispersal of Plants throughout the World*. Pp. xx + 744, with 22 plates. Price £3. 3s. 0d. Lovell Reeve & Co., 1930.

In any attempt to correlate vegetation with environmental conditions we are always confronted with the question as to how far the plant community and its habitat are in equilibrium at a given time. An important factor in the attainment of this equilibrium is the efficiency of dispersal, upon which in large measure depends whether or no those species most suited to a particular habitat arrive there at the appropriate phase of successional development. To every ecologist, therefore, the facility of dispersal of species must be of extreme interest.

The literature of the subject is very extensive, and is by no means compassed by the bibliography of about 500 references to the more important papers cited at the end of Mr Ridley's book. In addition to these there are, however, a number of references in the body of the text to papers of a more special character. Botanists in general and ecologists in particular are placed under a debt to the author, who has brought together in these pages a mass of published data together with numerous personal observations.

The subject-matter is classified according to the agencies of dispersal. The first chapter treats of dispersal by wind, and here the non-specialised and specialised reproductive organs dispersed in this way are considered in order according to the character of the structures involved. Under each heading a number of examples are described. This section occupies 162 pages and includes some data obtained by the author as to the distance of flight of winged fruits and seeds. The fruits of *Carpinus betulus* are given as being carried 100 yards from a tree 25 ft. high, those of *Fraxinus excelsior* 134 yards from a 20 ft. tree, whilst the seeds of *Pinus alba* were blown from trees 100–200 ft. high a distance of 880 yards. Mr Ridley stresses an important fact in emphasising the value for wind dispersal of even slight projections upon the reproductive body, which, by raising the fruit or seed away from the ground on which it has come to rest, permit of its being more readily caught up again by gusts of wind.

The second section of 171 pages treats of dispersal by water. Here the importance of rain-wash is stressed, particularly as an accessory to other means of dispersal. The data obtained by Praeger, Guppy and others respecting the time of flotation of various fruits and seeds are quoted and a number of examples described, including the coco-nut. The author takes the view that though human agency is largely responsible for the dispersal of this species, nevertheless its distribution is to some extent the result of sea-borne fruits.

Dispersal by animals and man occupies 326 pages and is treated under the headings of dispersal by birds, reptiles, batrachians, fish, insects, etc., dispersal by adhesion, and dispersal by man. Other shorter sections deal with mechanical dispersal, with island floras, and with the dispersal of orders and genera.

It is unfortunate that the index, though consisting of some 32 pages of small type, is not as complete a guide to the contents of this book as one could wish in a work that will doubtless become a standard work of reference on this subject.

The author's point of view, as indicated by the phraseology, is somewhat teleological. Thus of the Cruciferae the author writes: "It seems probable that the object of the flattening of the fruit... allows a freer play to the enlarged replum to throw the seeds further away when the wind strikes it." The bias towards seeing an objective in the structural modifications which a fruit or seed exhibits is perhaps responsible for the fact that the author's opinions sometimes seem more definite than the stated evidence would appear to warrant.



Thus of *Linaria vulgaris* the author states that "certainly its extreme abundance in Europe is mainly due to its winged seeds." Since, however, the percentage germination of this species is normally extremely low, whilst its power of vegetative spread by adventitious shoots from the roots is exceptionally high, the word "certainly" would appear to require more justification. So too one can hardly agree that the evidence quoted makes it "tolerably clear" that plumed seeds and fruits can fly quite 1000 miles at a single flight.

But if we cannot always concur with the author's opinions, we have here the data on which those opinions rest, and must feel both admiration and gratitude for the provision of such a mine of information which will be an indispensable book of reference to the ecologist.

E. J. SALISBURY.

**Shelford, Victor E.** *Laboratory and Field Ecology: The Responses of Animals as Indicators of Correct Working Methods.* Pp. xii + 608, with 219 text-figures.  $9\frac{1}{2} \times 6\frac{1}{4}$  in. London, Baillière, Tindall and Cox, 7 & 8 Henrietta Street, Covent Garden, London, W.C. 2, 1929. Price £2. 5s.

In 1913 Prof. Shelford published his book on *Animal Communities in Temperate America*. This book, which so clearly and attractively set forth the problems of animal ecology, must have drawn many who had previously only been naturalists into the more scientific study of animal communities and of the habitats in which they live. It certainly had this effect on the present reviewer. We might perhaps wonder why no naturalist, during the hundreds of years in which biology has been studied, had attempted to give more precision to his vague descriptions of environmental conditions. The present book is to some extent an answer to this question, since it shows very clearly that the progress of animal ecology has greatly depended upon the parallel development of physics and chemistry, and of technical inventions, without which it is impossible to make quantitative analyses of animal environments. Prof. Shelford's latest book, published seventeen years after the other one, seeks to supply the animal ecologist with a manual of technical methods for determining the reasons why each species of animal has a particular range and habitat. It deals more particularly with the inanimate environment, very little being said about the relation of species to each other and to plant life. The author adds, however, on p. 7, a warning that attention to pure "autecology" tends towards artificial treatment, since every animal in nature is part of an elaborate community of other species.

At first sight the reader will be somewhat daunted by the appearance of this book, which devotes such a large proportion of its space to technical descriptions of apparatus for experimentation. Thus, an appendix states that the student of ecology will be able to exercise a fair control over conditions if he is equipped with one hydroturbine air compressor, one  $\frac{3}{4}$  horse-power electric motor, four incubators, three thermostats, three electric fans, three thermographs, and three hygrographs, and several other things, costing in all about £250, apart from housing and overhead running costs. It should be realised, however, that the apparently overwhelming importance given to apparatus, and the comparatively small space given to animals themselves, is all part of a plan to reproduce exactly in the laboratory the climatic or aquatic conditions existing in the field. The author points out the fallacy of keeping animals under constant conditions, and the great importance of simulating the real variations of climate under controlled conditions. With this aim in view, he describes in detail the methods of controlling temperature, humidity, light, etc., and of applying these methods in order to determine the reactions of animals to environmental gradients, the range of activity, the rates of reproduction, and other processes. He believes that by these methods of experimentation it will be possible to understand enough about the limiting factors in

animal habitats to predict with accuracy, and also ultimately to explain in terms of physiological processes the behaviour and distribution of the animals themselves.

The book is throughout inspired with a belief in the possibility of treating animals as very complicated machines, and the possibility of animals being more than this, in other words, the possible *elasticity* of animal behaviour is not contemplated. It seems likely that this bias may be due to the author's particular interest in insect ecology, exemplified in his classical paper on the habitat reactions of tiger beetles (*Cicindela*) and his later experimental studies of the codling moth.

The style of the book is rather difficult, and follows the tradition of many American scientific books in placing undue emphasis upon the importance of technical terms and logical classification. Similarly, the English reader will find continuous reading hampered by the absence of connecting links between sentences, so that these resemble rather the bullets shot out from a machine gun, all effective if they reach their mark, all separate, but all from the same gun. In consequence the book remains rather a manual for reference than a text-book for general reading in ecology. But it is a manual which will remain of the greatest value and importance for many years: Prof. Shelford has a vision of animal ecology as an exact quantitative science, and if the results of this type of ecological work are still in an early stage, and remain uncoordinated, no one can doubt their importance in the future. With the results of his long and arduous investigations now before them, animal ecologists are in a position to apply sound methods to the problems which he was the first to bring vividly before them.

CHARLES ELTON.

## VEGETATION OF THE BALKAN PENINSULA.

### *The Plant Geography of Eastern Thrace.*

One of the most interesting areas of the Balkan Peninsula is the Strandja Dag in eastern Thrace. These hills are partly in Bulgaria, partly in Turkey. The Bulgarian parts have been visited by Stefanoff who has published an important phytogeographical paper<sup>1</sup> on his researches. Mattfeld<sup>2</sup> has more recently spent several weeks investigating the central portion of the hills but, unfortunately, for political reasons, was not allowed to make a complete survey of the massif. (His coloured map is misleading in this respect.)

Geologically the Strandja is an old mountain mass composed of Palaeozoic, and probably Precambrian, schists and gneisses, with granites and syenites. In the north and south Cretaceous-Eocene limestone unconformably covers the older rocks. This is a similar formation to that recorded for the Paphlagonian mountains by Nowack. Although exact meteorological data are not yet available, it seems probable that the climate of the Strandja area is different from that of the greater part of Thrace and is certainly not typically Mediterranean.

Mattfeld's observations on the plant communities add considerably to our knowledge of the plant life of eastern Thrace but, unfortunately, he has not attempted a clear classification. He describes the coastal dunes, brushwoods (especially oak-scrub and a kind of pseudomacchia<sup>3</sup>), steppe-like heaths, black pine woods, oak woods, stream-side woods (of *Quercus*

<sup>1</sup> Stefanoff, B. "Gorskit formacii v severna Strandza." (The forest formations in the northern parts of the Strandja mountains.) *God. na Sofijski Universit.* 20, ii, 1924.

<sup>2</sup> Mattfeld, J. "Die pflanzengeographische Stellung Ost-Thrakiens." *Verh. Bot. Ver. Brandenb.* 71, 1, 1929.

<sup>3</sup> Mattfeld retains the term "pseudomacchia" but extends its use to include brushwood intermediate between macchia and typical pseudomacchia. (See Turrill, *The Plant-Life of the Balkan Peninsula*, pp. 149, 155, Oxford, 1929.)

*conferta*, *Q. sessilis*, and other species of oaks, *Fraxinus oxycarpa*, *F. pallisae*, *Ulmus campestris*, *Alnus glutinosa*, and *Populus tremula*) rich in liane growths of *Smilax excelsa*, *Periploca graeca*, *Vitis silvestris*, and *Clematis vitalba*, and Colchic woods of the higher hills with *Fagus orientalis* and *Carpinus betulus*, frequently with *Rhododendron ponticum* as undergrowth. The author devotes some pages to a discussion of the general distribution of some of the phytogeographically more important species, such as *Calluna vulgaris*, which occurs in masses in this very isolated outlier of its distributional area, *Rhododendron ponticum*, *Prunus laurocerasus*, and *Fagus orientalis*.

Corresponding with the climate the vegetation of eastern Thrace cannot be described as on the whole Mediterranean. The extreme winter temperatures experienced in eastern Thrace are probably the most important limiting factors to Mediterranean plants and especially to the evergreen brushwoods, which are only found sparsely and discontinuously on the coast. The oriental beechwoods of the higher parts of the Strandja and of the ravines are similar to the woods of Colchis and of the areas bordering on the Black Sea in northern Asia Minor. Contrasting with the beechwoods, the oakwoods, usually on the lower slopes, are closely related to the oakwoods which have so wide a distribution throughout the Balkan Peninsula, and which are in part an extension of the Central European oakwoods. The steppe vegetation of the Ergene basin is closely related to that of central Anatolia. There are thus four phytogeographical elements represented in eastern Thrace: the Mediterranean (which is dominant in the Gallipoli Peninsula, outside the area visited by Mattfeld), the Anatolian steppe, the Central European, and the Colchic woodland. The great floristic importance of Asia Minor is everywhere apparent.

W. B. TURRILL.

### *Thessalian Olympus.*

Hayek, A. "Ein Beitrag zur Kenntnis der Vegetation und der Flora des thessalischen Olymp. Mit Beiträgen von Dr H. Handel-Mazzetti." *Beih. Bot. Centrbl.* 45, 220-328, Dec. 1928.

The Thessalian Olympus, famous in Greek mythology and one of the most beautiful of mountains, has a special botanical interest in having the second highest<sup>1</sup> peak (2918 m.) and being the highest mountain mass of limestone in the Balkan Peninsula. The present account of the flora and vegetation is based on visits paid by the late Dr Hayek (spring of 1926) and Dr Handel-Mazzetti (July 1927). A systematic list includes records of all the species known from Olympus, whether collected by these authors or by Heldreich, Orphanides, and the few other previous collectors. The descriptions of plant communities are by Hayek with comments by Handel-Mazzetti.

The following scheme is followed in classifying and describing the types of vegetation:

#### I. Forests.

##### (a) Deciduous.

Stream-side woods dominated by *Platanus*.  
Summer-green oakwoods.  
Beechwoods.

##### (b) Coniferous.

Black pine woods.  
Firwoods.  
*Pinus heldreichii*<sup>2</sup> woods.

<sup>1</sup> It is exceeded only by Mt Mus Alla in the Rila Planina of the Rodopes, 2924 m.

<sup>2</sup> *Pinus heldreichii* Christ, sensu Hayek = *P. leucodermis* Ant.

## II. Shrub communities.

## A. Evergreen.

1. *Macchia*.True *macchia*.*Quercetum cocciferae*.*Buxetum sempervirentis*.

## 2. Summer-green stream-side brushwood.

## III. Grass communities.

Marshy meadows.

Steppe-like meadows.

Pre-alpine meadows.

Alpine mats.

(a) *Seslerietum nitidae*.(b) *Seslerietum coerulantis*.(c) *Alopecuretum gerardi*.IV. Herb<sup>1</sup> communities.

## 1. High herb communities.

## 2. Rock flora.

(a) Association of *Inula candida*.(b) Association of *Ballota acetabulosa*.(c) Association of *Aubrietia deltoidea*.

(d) Subalpine rock plants.

(e) Alpine scree flora.

## V. Lichen associations.

The flora is shown to be essentially Mediterranean, and even that of the higher altitudes is related to the flora of the Greek mountains and thus to the lowland flora of the southern parts of the Balkan Peninsula (apart from relict endemics), and is, therefore, quite distinct from that of the Central European mountains. The reviewer has protested against the ambiguous use of the word "alpine" in phytogeographical literature, and the confusion which can arise in the mind of a reader is well illustrated in this paper where it is shown that the alpine (i.e. the high mountain) flora (of Olympus) has no genetic connections with the Alpine flora (i.e. the flora of the Alps of Central Europe). The highly endemic nature of the high mountain flora of the southern parts of the Balkan Peninsula is clearly related to its origin *in situ*, while the flora of the Alps is of mixed origin. The beech and a number of "*Buchenbegleiter*," and also *Quercus sessilis*, represent a spread of Central European types into an essentially Mediterranean flora.

W. B. TURRILL.

*Croatia.*

**Horvat, Ivo.** "Vegetacijske Studije o Hrvatskim Planinama" (Vegetational studies in the Croatian mountains). Croat with German summary. *Bull. internat. de l'Acad. Yougoslave des sci. et des arts. Cl. sc. math. et nat.* 24 (separate, pp. 1-88), 1930.

The Croatian mountains belong to the Dinarides and form a natural bridge between the Slovenian Alps and the mountains of the western parts of the Balkan Peninsula. Geologically

<sup>1</sup> The word "forbs," meaning herbs other than grasses, might be used with advantage to translate the German *Stauden*.

they are formed of Mesozoic limestones and dolomites with only slight outcrops of older rocks. Karst phenomena are much in evidence. The highest peak is in the Velebit (Vaganski vrh 1798 m.).

In the South Croatian mountains a mixed forest of beech, fir, and spruce (850–1350 m.) is followed by beech scrub generally surrounded by a girdle of *Pinus mughus* which forms the limit of woody vegetation. The present account deals mainly with the communities above this last. These are classified as follows:

Order: Seslerietalia tenuifoliae.

Group: Seslerion tenuifoliae.

*Carex firma* Association.

*Carex laevis*-*Helianthemum alpestre* Association.

*Carex laevis*-*Helianthemum balcanicum* Association.

*Sesleria tenuifolia*—*Carex humilis* Association.

Group: Festucion pungentis.

*Festuca pungens* Association.

Order: Caricetalia curvulae.

Group: Nardion strictae.

*Nardus stricta* Association.

*Leontodon hastilis* community.

The communities are described in detail, the ecological characteristics and floristic composition being also tabulated under the headings: altitude, exposure, slope, pH, size of association-individuals, size of quadrats, characteristic species, accompanying species, and occasional species. The comparative studies led to the interesting conception of sociological vicarism. Sociological vicarists are such taxonomic units as have analogous sociological function in diagnostic, syngenetic, and synecological respects in different communities of the same rank, irrespective of their systematic relationship.

The variety of existing communities in the higher altitudinal zones of the Croatian mountains cannot be entirely explained by local existing climatic differences. Exposure to or protection from the bora (*bura*) and scirocco (*jugo*) is an important factor, as is also the influence of man. Suppression of woody growth always leads to a succession (regression) whose vegetational stages show greater and greater tolerance of acidity and reach a climax in the Nardetum.

W. B. TURRILL.

**Morton, F.** "Beiträge zu einer pflanzengeographischen Monographie der Quarnerinsel Cherso." *Botanisches Archiv*, 24, 128–177, 1929.

The Quarnero district and the islands in the bay of the northern Adriatic separating the peninsula of Istria from South Croatia, are of exceptional phytogeographical interest because of the transitions they show between the Mediterranean and Transalpine (essentially Central European) floras and plant communities. The nature of these transitions is clearly indicated in this careful study of a limited part of the island of Cherso. The southern part of Cherso is Mediterranean, the northern Transalpine, and the central transitional. The great destructive and modifying influence of man is emphasised and most of the communities described are secondary. The methods used in studying the vegetation are adopted from the works of Braun-Blanquet and a large number of small "associations" are classified into the six "formations" of the garrigue, the mixed wood, the submediterranean brushwood, the submediterranean stony pasture, the karst wood, and the Mediterranean dry grassland. Lists of species, classified into layers of vegetation, with their degree of cover or quantity, and their sociability, are used to define the associations.

W. B. TURRILL.

## BRITISH ECOLOGICAL SOCIETY

### SOIRÉE AT EAST LONDON COLLEGE.

On Friday evening, January 9th, the night before the Annual General Meeting, the members of the Society were entertained at a Soirée in the Botanical Department of East London College.

The reception by Prof. and Mrs Fritsch took place from 8 to 8.30 p.m., after which the numerous exhibits were inspected. These included the following: an exhibit of Stream Algae by Prof. Fritsch and Mr Butcher; Plankton from the Transvaal exhibited by Miss Rich; Phytoplankton from the Thames exhibited by Mr Rice; an exhibit of Algal Periodicity by Mrs Howland; and of the Algae of Salt Marshes by Dr Nellie Carter. Messrs Owen and Paul Richards exhibited photographs illustrating the work of the Oxford Expedition to British Guiana; and Mr E. Milne-Redhead showed aerial photographs of Northern Rhodesian vegetation. Dr Pearsall exhibited maps showing the vegetational changes in Esthwaite Water since 1914. Dr T. A. Sprague exhibited an interesting series of habitat forms of *Linum catharticum* showing remarkable diversity of habit and appearance; and Mr F. Ballard a series of herbarium specimens of plants collected in Sark. Apparatus for ensuring effective circulation and aeration in marine aquaria was exhibited by Dr A. J. Grove.

During the evening members were provided with light refreshments by the generosity of the Governors of the College.

### ANNUAL MEETING, JANUARY 1931.

The seventeenth Annual Meeting was held in the Botanical Department of East London College on January 10th, 1931, when the President, Prof. F. E. Fritsch, occupied the chair. The minutes of the previous meeting were read and confirmed. The Honorary Secretary then read his Report on the work of the Society during the year.

### HON. SECRETARY'S REPORT FOR THE YEAR 1930.

The sixteenth Annual Meeting was held on January 4th in the Botanical Department of the University of Leeds by kind permission of Prof. Priestley. On the previous evening Prof. and Mrs Priestley entertained the members at a Soirée at which a number of exhibits were shown, and on the Sunday following Dr Pearsall led an excursion to some oakwoods in the neighbourhood. The thanks of the Society are due to Prof. Priestley, Mrs Priestley, Dr Pearsall and others who contributed to a most successful and enjoyable meeting.

At Easter a joint meeting with the Bryological Society was held at Wareham, and it is to be regretted that more members of this Society did not avail themselves of the opportunity of seeing bryological communities under the guidance of specialists.

Owing to the numerous fixtures during the summer, including two International Congresses, a summer meeting was not held.

The annual joint meeting with the British Mycological Society was held in October at Aldbury when we were again indebted to Mr Ramsbottom for leading the excursion.

Two numbers of the JOURNAL have been issued, in February and August respectively, together consisting of 392 pages, supplements of 34 pages and 15 plates.



The Society's transplantation experiments are being continued at Potterne under the direction of the Committee consisting of Sir A. W. Hill, Mr E. M. Marsden-Jones, Mr C. G. T. Morison, Prof. F. W. Oliver, Prof. E. J. Salisbury, Mr V. S. Summerhayes, Prof. A. G. Tansley and Dr W. B. Turrill. The first report on these experiments was published in the last number of the JOURNAL.

We deeply regret to record the death of Prof. C. E. Moss, who was one of the members of the original British Vegetation Committee and whose valuable work on the vegetation of Yorkshire, Somerset and the Peak district did so much for the advancement of the primary survey of British vegetation. An Obituary Notice appears in the present issue.

Thirteen members have resigned, or been removed from the list of members owing to non-payment of subscriptions, and the same number of new members have been elected, giving an unchanged total membership of 254.

E. J. SALISBURY.

The President announced that the Council had decided to begin the formation of the nucleus of a library, a collection of pamphlets, maps and photographs, and had accepted the generous offer of the Keeper of Botany at the British Museum (Mr Ramsbottom) to house the collection in his Department for the present (see p. 232 of the present issue).

Prof. Tansley said that the Society had reached a critical stage in its development, in regard especially to finance, and by that he did not mean "dangerous"—on the contrary its prosperity was greater than it had ever been—but a stage requiring careful judgment as to future policy. There was now a surplus of well over £1000 if the current market value of investments were considered. About £900 of this had been accumulated in the last six years. The surplus could be regarded as derived entirely from the sale of back numbers of the JOURNAL, which had realised £1302 during the six years, or an average of about £217 per annum. Of this we had on the average saved £150 and spent £67 in each year. He had always regarded the accumulated surplus as a reserve, of the nature of a sinking fund, to provide for the replacement of those back numbers which would shortly be exhausted. It was of essential importance to replenish these so as to keep complete sets available for sale, because the larger portion of the receipts from sales of back numbers and the most stable income from this source was represented by sales of complete sets. These were bought especially by libraries and institutions which became subscribers, and the sales depended on the maintenance and increase of the JOURNAL's prestige and usefulness. This reserve fund was none too large for its purpose 2 or 3 years ago, but thanks to recent improvements and cheapening of the "photostatic" process of reproduction and to the continued steady sale of complete sets, we should now be in a position, if the present rate of sale continued, to find the few hundred pounds that would be required for replenishment during the next five or six years quite easily, and possibly have free income for fresh activities in addition. The Council had decided to enlarge the JOURNAL to a small extent, and to take the first steps towards the foundation of a library of books, pamphlets, maps and photographs for the use of members. It would not, however, be possible to form a fully equipped library with all desirable facilities for some years yet. And the possibility that the market for the sale of sets of the JOURNAL might shortly be saturated, or at least slacken off, must always be kept in mind. It would therefore be necessary to proceed cautiously in embarking on new expenditure, for we were still not quite, though we were now very nearly, covering the current cost of the JOURNAL from current subscriptions.

The following officers were then elected:

*Vice-President:* Prof. J. R. MATTHEWS.

*Hon. Secretary:* Prof. E. J. SALISBURY.

*Hon. Editor:* Prof. A. G. TANSLEY.

*Hon. Treasurer:* Mr H. BOYD WATT.

*Council Members:* Mr C. S. ELTON and Mr A. J. WILMOTT.

# BRITISH ECOLOGICAL SOCIETY

## REVENUE ACCOUNT FOR THE YEAR 1930

### Income

Subscriptions received including arrears	£	s.	d.
Less prepayments for 1931 ...	290	14	2
	12	8	6
Interest on Investments ...	278	5	8
Interest on Deposit Account	25	18	7
<i>Journal of Ecology</i> —Sales, etc.:	2	16	8
Current volume, xviii, 1930 ...	454	13	0
Back volumes and parts ...	248	3	2
Advertisements ...	1	14	10
Authors' contributions towards cost of plates ...	10	0	0
Repayment by B.E.V.C. (towards cost of separate issue of Supplements)...	15	0	0
Credit on account of overcharge 1929	729	11	0
British Vegetation Committee—Sale of Reprint	58	9	0
	2	3	

£1095 3 2

### BALANCE SHEET AT 31st DECEMBER, 1930

#### Liabilities

Subscriptions prepaid for 1931 ...	£	s.	d.
<i>General Revenue Account</i> —Balance of Funds:	12	8	6
Surplus at 31st December, 1929	685	18	1
Surplus from Revenue Account 1930...	303	5	0
	989	3	1

£1001 11 7

I have examined the accounts of the year ending 31st December, 1930, and certify them to be a correct statement and that all the vouchers are in accordance with receipts and payments shown therein.  
(signed) ROBERT PAULSON.

### Expenditure

<i>Working Expenses:</i>	£	s.	d.
Printing circulars, etc.	9	5	0
Postages	4	12	4
Bank charges	4	6	
Clerical assistance (Secretary and Treasurer)	15	0	0
Transplant Committee Fund, Grant	29	1	10
Soirée Expenses	5	0	0
<i>Journal of Ecology:</i>			12 6
Paper, Printing, Illustration, etc.	609	19	1
Binding	8	10	3
Postage, etc.	32	17	1
Insurance of Stock	1	18	0
Publishers' Commission	95	6	4
Back Parts Purchased	6	18	1
Reprints (100) of "Experiments at Potterne"	1	15	0
Balance—Surplus of Income over Expenditure—Carried to Balance Sheet ...	757	3	10
	303	5	0
	£1095	3	2

#### Assets

<i>Westminster Bank—Credit Balances:</i>	£	s.	d.
Current Account	35	18	7
Deposit Account	50	0	0
<i>Investments:</i>			85 18 7
£700 5 % War Loan 1929/47 at cost ...	717	3	0
(Market Value at 31st December, 1930, £724. 10s. 0d.)			
£200 5 % Conversion Loan 1924/64 at cost	198	10	0
(Market Value at 31st December, 1930, £212. 0s. 0d.)			
	915	13	0
	£1001	11	7

NOTE. A further asset is the unsold stock of the *Journal* held for the Society by the Publishers.  
(signed) HUGH BOYD WATT,  
Hon. Treasurer.

The PRESIDENT then delivered his address entitled: "Some Aspects of the Ecology of Fresh-water Algae" (which will appear in the second issue of the JOURNAL for 1931).

On the proposition of Prof. Tansley, seconded by Dr Woodhead, a unanimous vote of thanks was accorded the President for his valuable address, the speakers paying a tribute to Prof. Fritsch's services to the study of fresh-water biology in this country.

Dr GODWIN then gave an account of the water relations of fens, taking the example of Wicken Fen near Cambridge, the seasonal changes in whose water table had been very thoroughly studied. This shows a low level and a saucer-shaped surface from the beginning of June to the middle of September, corresponding with the period of maximum transpiration of the vegetation. The fall in June and the autumn rise, which results in a high flat table during winter and spring, are independent of the rainfall. The communities of the prisere (Phragmitetum, Cladietum and "carr") appear to be determined by the height of the water level in winter and not by water deficiency in summer. Two communities, however (Cladio-Molinietum or "mixed sedge," and Molinietum or "litter") have no place in the prisere and must be regarded as examples of *deflected succession* resulting from the incidence of periodic cutting on the fen vegetation, which changes the course, though it does not stop the major reaction (rise of peat level) of the succession. In the discussion which followed Prof. Griffiths, Mr H. S. Thompson, Prof. Matthews, Prof. Salisbury, and Dr A. S. Watt took part.

The meeting then adjourned and members were entertained to luncheon by the Governors of East London College.

After the adjournment the Hon. Treasurer, Mr Boyd Watt, presented the Balance Sheet and Accounts, which were adopted. These showed a balance for the year of £303. 5s. On the proposition of the President a vote of thanks was accorded to Mr Paulson for acting as Hon. Auditor of the Accounts. On the proposition of Prof. Tansley, seconded by Mr Ramsbottom, a vote of thanks was passed to the Hon. Treasurer for his careful custody of the Society's finances.

Dr McLUCKIE then gave an account of "Some Aspects of the *Eucalyptus* Forests of Eastern Australia." The *Eucalyptus* forests occupy about 90 per cent. of the forested area of the continent. The most important of the other natural forests are rain forest, littoral swamp forest, and *Casuarina* forest. The first-named colonises the sheltered valleys, gorges, and basaltic residuals of Eastern Australia, where it competes successfully with the *Eucalyptus* forests of poorer soils. In the north it closely resembles tropical rain forest, but towards the south there is a continual decrease in number of species and proportion of epiphytes. The *Eucalyptus* forest is regarded as a climatic climax and the rain forest as an edaphic climax. The littoral swamp forest occurs on the tropical coasts and estuaries, whilst *Casuarina* forest is found on alluvial soils, as a fringing forest on river flood plains, and in limited areas of sandy soils.

*Eucalyptus* forests occur from sea level to the tree limit at 6300 ft. and are remarkable for their dominance by members of a single large genus of very varied habit, ranging from the giant *E. regnans* to the shrub-like *E. stricta*. Many of the three hundred species are very variable but all exhibit pendulous foliage and the shade cast is slight. The specific composition of the lower strata does not vary with that of the dominants. After burning there is rapid regeneration both by seed and suckers, and all strata, especially the shrubs and trees, exhibit a striking capacity for rapid growth. The controlling factors are rainfall, temperature, air-drainage, exposure, and soil, and these are influenced by the physiographical features of the continent. The great dividing range, 2000-7300 feet in altitude, runs parallel with the east coast at a distance of 40-100 miles. This range separates the eastern coastal belt of high rainfall (30 to 60 inches) with a high percentage reliability, from the central basin of low and erratic precipitation. The forested areas occupy soils derived from a great variety of rocks; the most sclerophyllous type, covering thousands of square miles in New South Wales, occurs on sandstones and exhibits low humus and water contents. The dominants

are such species as *E. piperita*, *E. haemastoma*, *E. eugenoides*, *E. corymbosa*, *E. siberiana*, *E. angophora*, and *E. lanceolata*. A sclerophyllous shrub stratum is very typical and in this Proteaceae, Leguminosae, Myrtaceae, and Rutaceae are conspicuous features. After forest fires numerous seedlings develop of *Hakea*, *Grevillea*, *Leptospermum*, *Boronia*, etc., of which a few only attain maturity. Repeated fires bring about continuous reduction in the canopy of the tree layer with consequent increase of insolation and of photophilous shrubs. *Eucalyptus* forest on the basalt differs physiognomically, and possesses few species, e.g. *E. blaxlandi*, *E. goniocalyx*, *E. oreades*, and *E. viminalis*. The trees are closer together, photophilous shrubs are replaced by mesophytes with larger leaves, and there is a continuous ground carpet of ferns and mosses. On the shale two types of *Eucalyptus* forests occur, namely the mixed forests in the sheltered valleys, with *E. pillaris*, *E. lanceolata*, *E. paniculata*, etc. and the exposed coast plain type which is lower and more sclerophyllous. On the granite the most typical forest is dominated by *Eucalyptus coriacea* associated with congeners.

Prof. Tansley, Prof. Salisbury, Mr Sager, and Dr Godwin took part in the discussion, and a vote of thanks was accorded to Dr McLuckie for his interesting and useful epitome of Australian forest vegetation.

Mr E. MILNE-REDHEAD gave a general account of the vegetation of part of the Solwezi and Mwinilunga Districts of Northern Rhodesia. *Brachystegia* woodlands dominate this area except for the southern and western parts of the Mwinilunga district where *Brachystegia* is replaced as the dominant by *Cryptosepalum* on the Kalahari sand of the Mavunda country. A narrow margin of bare soil usually separates the forest from the open valley grasslands ("dumbos"), which are a characteristic feature of the country, and evergreen fringing forests are frequent along the river banks. The pronounced influence of the native "shifting" cultivation was emphasised, and also the importance of termites, whose very numerous old nests often bear a vegetation totally distinct from that around. The communication was illustrated by aerial photographs kindly lent by the Aircraft Operating Co., Ltd.

On the proposition of Mr Ramsbottom a hearty vote of thanks was accorded to Prof. Fritsch for the hospitality of the Botanical Department, and the Hon. Secretary was asked to convey to the Governors of East London College the Society's appreciation of the hospitality they had enjoyed. Prof. Fritsch then vacated the chair, which was occupied by the Vice-President, Prof. Matthews.

Messrs O. W. and P. W. RICHARDS then read a joint communication on ecological observations made during the Oxford University Expedition to British Guiana in 1929 (led by Major R. W. G. Hingston).

Mr P. W. RICHARDS said previous work on tropical vegetation had been extensive rather than intensive and had been strikingly lacking in exact data. The ecological objective on the Guiana expedition was to make as definite a description as possible of a limited area of rain forest in the neighbourhood of Moraballi Creek on the Essequibo, 6° north of the equator, an area which had a fairly typical equatorial climate with two not very clearly marked wet and dry seasons in the year. Among the mass of facts collected the demonstration that the forest was not floristically homogeneous was, perhaps, of most general interest. Five distinct types were recognised and were found to be related each to a particular type of soil. Counts of all the trees on sample plots were made for each type of forest; identifications were by means of native Indian names, many, though not all, of which were shown to be perfectly trustworthy. Comparison of the plots showed that the high forest types, when arranged in order from that developed on soil of highest to that on soil of lowest water-content, form a remarkably regular series; some characteristics, e.g. number of trees per unit area, increase steadily from one end of the series to the other, others increase or diminish from each end towards the middle. Thus there is a high degree of dominance of single species in the two extreme members of the series and a mixture of species without any clear

dominance in the middle. The occurrence of dominance seems to be related to relative unfavourability of the habitat.

In the widespread occurrence of dominance and in other respects the Guiana rain forest seems to be exceptional, but it is impossible to say how absolute is the apparent contrast till more exact data are available from other rain-forest regions.

Mr O. W. RICHARDS said that one of the principal objects of the expedition had been to discover to what extent there was a real tree-top zone of animals, such as had been described in general terms by the early travellers on the Amazons. Amongst birds such zonation had already been partly established by Beebe's observations in British Guiana. The ornithologists of the Oxford expedition had extended these results, though the facts were not altogether simple owing to intercommunication between different zones. The insects presented a more difficult problem, since the species could not merely be observed but had to be captured. For this purpose it was necessary for the trees to be climbed, which was accomplished by the aid of Indian climbers. When once a rope had been passed over a high fork of a tree, it was possible to haul up either a block and tackle or a rope ladder allowing permanent access to the fork in question. Even then not every insect seen could be captured. "Light-traps" for catching insects at various levels were also employed and specimens obtained could be compared with those attracted to light at the ground level. To some extent also insects could be collected from trees immediately after felling. The fauna revealed by these methods had to be compared with that existing on the ground level in order to discover the extent to which the tree-top fauna was peculiar to its zone. It would not be possible to make this comparison in detail for some years owing to difficulties of identification, but it already appeared that certain striking forms were restricted to the higher levels.

The collecting done on the floor of the forest had incidentally led to the study of several small communities such as those inhabiting hollow trees or attracted to carrion, while a number of observations and photographs of the nesting habits of bees and wasps had also been obtained. These secondary results were likely to prove as valuable, eventually, as the actual data on zonation, though the latter could not be evaluated till the collections had been more fully worked out.

Prof. Tansley and Prof. Salisbury paid a tribute to the value of the observations made by the Messrs Richards and by Mr Milne-Redhead, and to the vivid and fascinating glimpses of new types of vegetation they had given the Society. The authors of these papers were to be warmly congratulated on the large mass of data they had obtained in the comparatively short periods at their disposal. The meeting then concluded.

E. J. S.



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PROPOSAL TO FORM A COLLECTION OF BOOKS, PAMPHLETS, MAPS  
AND PHOTOGRAPHS.

The Council of the British Ecological Society has decided to begin the formation of a collection of books, pamphlets, maps and photographs for the use of members. The state of the Society's finances now permits of some expansion of its activities, and though caution is needed before undertaking serious commitments, the proposed step seems justified by the existing financial position and the prospects.

The Society already possesses a small collection of mounted photographic prints of British Vegetation, but this has remained undeveloped for many years, and requires rearrangement, relabelling and continuous enlargement. There is also a possibility of acquiring in the near future another valuable collection of photographs of British vegetation. The Editor of the JOURNAL has a large and continuously increasing collection of pamphlets, now numbering nearly 4000, on vegetation and ecology, properly arranged and with a card catalogue of authors, and this he has always intended to give or bequeath to the Society if and when proper accommodation became available. The above would form a valuable nucleus for the Society's collection.

It has been suggested, also, that it would be of great advantage if surveyors of vegetation would deposit with the Society original manuscript maps made in the course of their work, as these often contain valuable data and indications which remain unpublished and might well be of great use to future workers.

Mr Ramsbottom, the Keeper of Botany at the British Museum, has generously offered to house at the Natural History Museum, for the time being, the beginnings of the proposed collection, and arrangements will be made to give members of the Society access to the photographs, books and pamphlets thus stored. This arrangement is only intended to be provisional, but it will greatly assist the Society in making a start with its collection.

Members of the Society and others, who have ecological photographs, maps, books, pamphlets or suitable journals (complete sets or considerable runs only), of which the best use is not being made, are invited to present them to the Society. They should be addressed to

**The British Ecological Society,  
c/o Department of Botany,  
British Museum (Natural History),  
South Kensington,  
London, S.W. 7.**

Formal acknowledgement of the receipt of such gifts will be made.

Eventually it may be possible to form a proper library of pamphlets and books, including journals, and a collection of photographs and maps. But this of course cannot be done until permanent housing can be obtained and the Society's assured income permits of proper upkeep and provision for continuous augmentation.



SOME ASPECTS OF THE ECOLOGY OF FRESH-WATER  
ALGAE<sup>1</sup>

(WITH SPECIAL REFERENCE TO STATIC WATERS)

By F. E. FRITSCH.

*(With five Figures in the Text.)*

In the following I propose to give a general account of the present position of our knowledge as regards the algal ecology of static fresh-waters. A good deal of attention is now being paid to flowing waters in this country in relation to pollution and, since it became necessary to narrow down the field of these considerations, it appeared most suitable to omit flowing waters and to confine my attention to standing water. This may be the more appropriate, since it is to be hoped that the present year will see the establishment of a fresh-water biological station on Lake Windermere.

One of the earliest attempts to classify fresh-water algal communities as a whole was made by G. S. West in 1916 (161) in the Cambridge Botanical Handbooks<sup>2</sup>. West had enjoyed unrivalled opportunities of becoming acquainted with the fresh-water algal flora of many parts of the world and this, combined with his extensive investigations on British Algae, afforded him a general view of algal habitats such as few others possessed. With few exceptions, however, he did not succeed in establishing a classification that could serve as a foundation for further investigations. As will be familiar, his main classification was into subaerial associations, associations of irrorated (or dripping) rocks, and aquatic associations, the last being further subdivided into those of swiftly running water, those of bogs and swamps, those of ponds and ditches, and those of pools and lakes. A perusal of these aquatic associations leaves one with very few tangible data for their separation or for the distinction of individual communities among them. The data provided are essentially floristic, and this is true also of a large number of so-called ecological accounts of the algal flora of various districts that have been published in the last two decades.

West and his father, however, made one very noteworthy contribution in the direction of a further elucidation of algal habitats. As a result of their extensive studies of British phytoplankton they arrived at the conclusion that the rich Desmid floras, comprising a large number of types in this country exclusively confined to the western region, corresponded geographically with

<sup>1</sup> Presidential Address to the British Ecological Society delivered at the Annual Meeting on January 10th, 1931.

<sup>2</sup> Cf. also 133, p. 196; 18; 19.



the precarboniferous rocks and occurred in waters characterised by a poverty of dissolved mineral salts. A number of these special types of Desmids were, moreover, shown to form a dominant feature of the plankton in many of the lakes found in these regions (161, p. 442; 162, p. 199). A Desmid plankton, first reported by these investigators from the Scottish lakes and subsequently found to occur also in the English, Welsh, and Irish lakes, was altogether a novelty in the study of phytoplankton, although later research disclosed its occurrence also in other parts of Europe (1, 2, 27, 46, 126, 134), as well as in America (125), the Victoria Nyanza (121, p. 28), and the Yan Yean Reservoir in Victoria (160). But the essential forward step lay in the bringing into line of this type of plankton with the geological characteristics of the basins within which it occurred.

Further insight into the factors causing the appearance of this peculiarly distinctive type of plankton was provided by Pearsall (104, 106, 107). His detailed investigations in the Lake District (cf. also 109) afforded corroboration of the fact already established by the Wests (163, p. 428) that the Desmid plankton is characteristic only of some of the lakes, whilst in others Diatoms and Myxophyceae play the principal rôle. It will be familiar that Pearsall was able to establish clearly that the Desmid plankton is restricted to lakes with a large percentage of rocky shore and showing little silt deposition, with *Isoetes* and *Nitella* as the dominant macrophytes, and with clear soft waters, poor in calcium and magnesium, but with a relatively high proportion of potassium and sodium; only a small part of the drainage system of such lakes is cultivated. Subsequently it was shown that, during the summer months, the water has a low carbonate hardness and pH, and relatively high phosphate and silica content (108).

A further important conclusion reached by Pearsall was that, on the assumption that at the close of the glacial epoch all these lakes were more or less uniformly rocky, those on the hardest rocks had changed least and showed relatively primitive characteristics, whilst those lying on softer strata had undergone more silting and therefore exhibited a later stage in development. It is these latter that lack the Desmid plankton typical of the former. Pearsall (104, p. 279) was able to establish a progression from a plankton dominated by Desmids (with abundant *Sphaerocystis Schroeteri*), via an intermediate stage with Diatoms (especially sp. of *Tabellaria*) dominant but Desmids still abundant, to one dominated by Diatoms with *Eudorina* and *Ceratium* abundant, and finally to an *Asterionella* plankton with codominant Myxophyceae. This progression was shown to go hand in hand with differences in the physical features before mentioned, in the quantity and quality of the macrophytes, and in the dominant fish. The more highly evolved lakes, with their plankton of Diatoms and Myxophyceae, show considerable approximations to the Danish lakes, well known through the investigations of Wessenberg-Lund (154), to those of the North German plain (7, p. 108 *et seq.*), and to many of

the pools of the Midlands (cf. 42, also 105), although never exhibiting the periodic abundance of the phytoplankton that is characteristic of these various waters.

In the meantime the classification of lake types was being approached on the continent from a somewhat different angle<sup>1</sup>. The vigorous pursuit of limnological studies in Germany and Austria, stimulated by the presence of active fresh-water biological stations at Plön and Lunz, and the fostering of similar researches by the Swedish fishery authorities, had led to the gradual accumulation of a wealth of detail relating to all aspects of the biology and physiography of European lakes. In 1919 Naumann (77) classified phytoplankton into the oligotrophic formation of waters poor in mineral nutriment (especially nitrates and phosphates) and typical of the more ancient rocks, and the eutrophic formation of waters with a richer content of electrolytes. These are distinguished on the basis of plankton productivity, the oligotrophic being characterised by a low, the eutrophic type by a high productivity, often obvious in distinctive coloration of the water (water flowers) by one or other organism (cf. also 83). The plankton of oligotrophic waters is in general, however, richer in species than that of eutrophic waters. Subsequently Thienemann (138, p. 202), in giving a synopsis of the essential differences between the two types of waters, states that in the oligotrophic type the phytoplankton is essentially green, while in the eutrophic type it is mainly blue-green<sup>2</sup>. In the third place Naumann distinguished a heterotrophic formation characteristic of waters rich in organic substance, either as a result of natural or artificial causes<sup>3</sup>. Naumann's classification was primarily based on the grouping of aquatic micro-communities into oligosaprobies, mesosaprobies, and polysaprobies by Kolkwitz and Marsson in 1908 (54).

Nordqvist in 1921 (99) established that the distinction between oligotrophic and eutrophic types could also be drawn with reference to the zooplankton of ponds. He showed (p. 76) that oligotrophic ponds are specially characterised by the dominance of Cladocera, the almost complete absence of Rotifers, and the small part played by the Copepods in summer; eutrophic ponds (p. 82), on the other hand, contain a large number of Rotifers and abundant *Cyclops*, while the Cladocera are the less frequent the more marked the eutrophic character.

A further line of attack was opened up by the investigation of the sediments (67, 82, 96) which differ markedly in quantity and quality in the two extreme types distinguished by Naumann. The scanty sediments of oligo-

<sup>1</sup> With reference to some of the older methods of classifying waters, see 91.

<sup>2</sup> Huitfeldt-Kaas (48, pp. 174, 181) had already previously suggested a classification into lakes with a plankton of Chlorophyceae and those with a plankton of Myxophyceae, the two types in general corresponding to the oligotrophic and eutrophic types of Naumann.

<sup>3</sup> In the light of subsequent work it does not appear possible to distinguish the heterotrophic clearly from extreme eutrophic types, and it is not taken into consideration as a separate category in the following matter.

trophic waters<sup>1</sup> are usually poor in organic substance (56, p. 661; 166, p. 264), while those of the eutrophic type are more abundant and rich in autochthonous organic material in process of decay, derived from the abundant plankton. These latter sediments typically constitute the grey to black "gyttja" and "Faulschlamm" (sapropel) of the Scandinavian and German workers respectively. Koppe (56, p. 662) describes such sediments as consisting of a greenish grey uppermost layer in which the remains of many planktons are still recognisable, succeeded by a thicker blackish grey middle layer which is the seat of intensive decay and is inhabited only by anaerobic Bacteria, and finally a greyish layer where decay is complete. Even in oligotrophic waters, however, a certain amount of gyttja can be deposited. Thus Haempel (44, p. 280) describes for the deep Attersee a homogeneous greyish green sediment which is perfectly odourless, but which apparently attains to an appreciable thickness (cf. also 66, p. 72).

While Naumann classes all the organic sediments of eutrophic waters under the one heading "gyttja," Gams (33, p. 291) distinguishes "Faulschlamm" (sapropel) (i.e. putrefying ooze) from it on the ground that true gyttja shows a marked coprogenous character (94, p. 702; 154 a, p. 437), since the bottom fauna plays a considerable part in its formation, while sapropel is formed only in marked absence of oxygen with the co-operation of polysaprobic and anaerobic organisms<sup>2</sup>; it occurs especially in small stagnant waters and is always rich in sulphuretted hydrogen and other gases (methane, etc.). The distinction thus drawn between the sediments of eutrophic waters is, however, according to Naumann (94) only one of degree, since sapropel is connected with gyttja by transitions. Gams also mentions that transitions between Cyanophyceous gyttja and sapropel are not rare. As regards the rate of formation of such sediments, Osvald (101) calculates for a *Pediastrum* sediment a deposit of 1.5 mm. and for a *Chroococcus* sediment one of 3–4 cm. per annum.

Sediments of a different kind are formed in moorland waters which, like the oligotrophic, are poor in electrolytes and have a scanty plankton, but are less transparent owing to their brown or yellow coloration. Thienemann and others distinguish these as a third, the dystrophic type, but Naumann (81, p. 11) regards them merely as a special category of the oligotrophic, characterised by the fact that there is abundant introduction of foreign organic material (cf. p. 247). In such waters the rich organic sediments are formed mainly by precipitation of the colloidal humus compounds introduced from outside. These brown sediments constitute the "Dy" or "Torfschlamm" (tyrfopel)

<sup>1</sup> In calcareous subalpine lakes the sediments may consist almost exclusively of precipitated lime fragments.

<sup>2</sup> This corresponds with the definition of "Faulschlamm" (sapropel) given by Lauterborn (60; 60 a, p. 400 *et seq.*); this term was used by Potonié (111, p. 101 *et seq.*) in a different sense and as synonymous with gyttja.

(i.e. peat ooze)<sup>1</sup> and have a very low nutrient value (cf. especially 96, pp. 52, 53); an alkaline extract has a more or less deep brown colour.

Utermöhl (148, 149) further distinguishes "Humusschlammseen" (i.e. lakes with a humus ooze), characteristically found in Eastern Holstein, from those of the typical eutrophic kind. They are relatively shallow and poor in lime. In these the sediments (56, p. 664) are not due to precipitation of humus colloids, but to the considerable introduction of dead foliage from the surrounding woods. This only decays in part forming a yellowish brown humus from which the mineral substances are completely absorbed (cf. also 55). Owing to the abundant mineral nutriment in the water these lakes, however, show the high plankton productivity of the eutrophic type, the plankton according to Utermöhl exhibiting a marked stratification with several different forms dominant at the same time in different layers of the water. It would seem, therefore, that one must recognise three types of eutrophic waters according as the sediments are of the nature of gyttja, sapropel, or humus ooze, the last being paralleled among oligotrophic waters by the dystrophic facies.

On most of these diverse sediments a distinctive flora (56) and fauna are to be found, rich in species in the oligotrophic, but much poorer in the eutrophic and dystrophic types; as regards quantity the fauna is poorest in the last-named. In the eutrophic type the richness of the bottom fauna is ascribed to the plentiful nutriment afforded by the rain of dead plankton, while in the oligotrophic type it appears to be due to the often abundant bottom flora of colonial green and blue-green Algae and Diatoms, to which Forel (30, p. 188) first drew attention. Lundbeck (64, p. 392 *et seq.*) distinguishes a number of types of oligotrophic and eutrophic lakes according to the nature of the bottom fauna, and relates these especially to the amount of humus present. He emphasises (p. 410) that, apart from the oxygen relations, the available nutriment and the amount of humus are of great importance, both for the metabolism of a lake as a whole and especially in relation to the bottom fauna. There can be no doubt that the oxygen relations very largely influence the nature of the latter (cf. 136) and we may therefore in the next place devote a little time to their consideration.

We owe to Birge and Juday (9) the first full elucidation of these matters. Working on the lakes of Wisconsin, they showed that, during the summer stagnation period, the bottom layers of the water show an oxygen deficiency as compared with the surface layers (cf. also 30, p. 98), which may be either slight or very considerable, a more or less extensive part of the hypolimnion being often altogether devoid of oxygen (*loc. cit.* p. 45). They ascribe this to the decay of the littoral vegetation and of foreign vegetable matter falling into the water and especially to the decay of the phytoplankton which, on reaching the colder and denser water of the hypolimnion, sinks more slowly

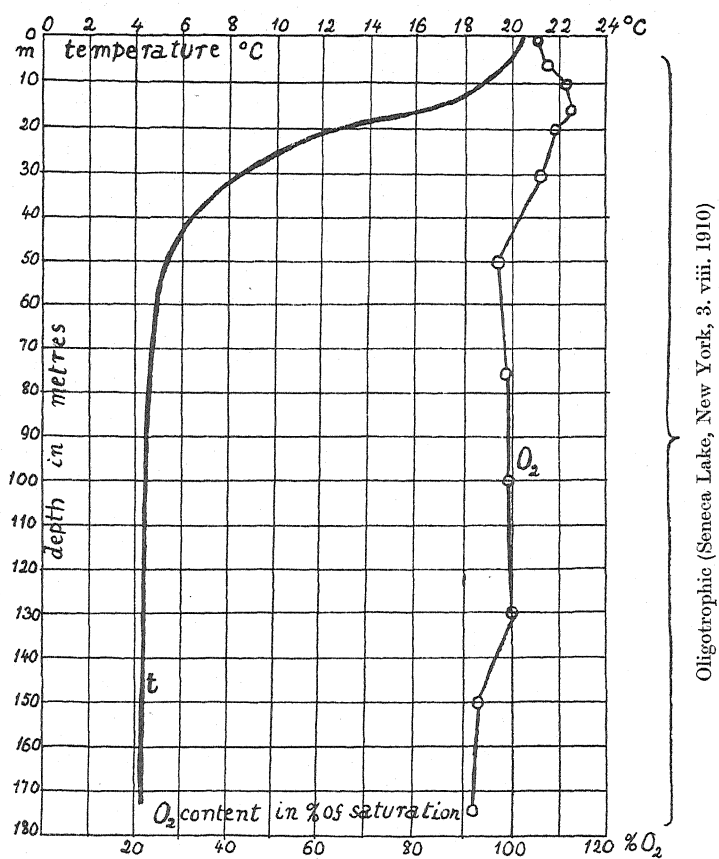
<sup>1</sup> The terms "gyttja" and "dy" were first introduced in the fundamental work of von Post (110, cf. also 111).

so that the oxygen consumption involved in its decay is spread over the whole of the hypolimnion. The extent of oxygen consumption in the latter will depend in the main on the amount of organic matter and on the relative volumes of epilimnion and hypolimnion, although other factors also come into play. In a subsequent communication dealing with the Finger Lakes of New York (10) they showed that certain of these (oligotrophic) exhibit a high percentage of oxygen in the hypolimnion at all times of the year.

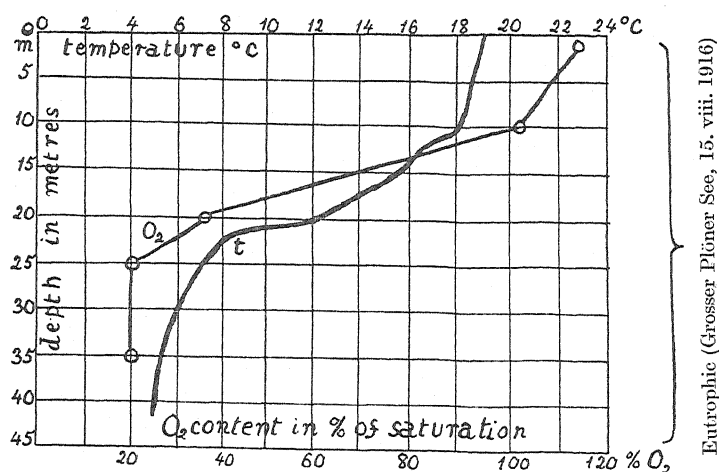
Thienemann working on the lakes of the Eifel (135) confirmed the results of Birge and Juday. He distinguished three types on the basis of their thermal and oxygen relations. Two of these are characterised by thermal stratification, showing a well-marked thermocline during the summer stagnation period. In the first (Fig. 1, above) there is a gradual decrease in the percentage of oxygen from the surface to the bottom, but even in the hypolimnion there is an appreciable oxygen content (usually 60-70 per cent. of saturation). In the second (Fig. 1, below) there is a sudden marked decrease in oxygen content in the region of the thermocline, and the lower part of the hypolimnion is poor in oxygen or, as in many of the Wisconsin lakes studied by Birge and Juday, altogether devoid of it. In the waters of the second type there is a sharp bend in the oxygen curve (cf. also 9, p. 50) when one reaches the thermocline (Fig. 1). Thienemann's third type (cf. also 9, p. 45) shows no thermal stratification and no obvious difference in the oxygen content of different layers. In a subsequent communication (137) this third type is not maintained, since it is regarded as resulting from shallowness of the water allowing of constant circulation, and the opinion is expressed that such pieces of water will probably be found in other respects to conform to one or other of the two remaining types. In the same paper Thienemann points out (p. 350) that these latter cover respectively the oligotrophic and eutrophic types of Naumann, since it is essentially the abundant plankton characteristic of the latter type that causes the marked decrease in oxygen content below the thermocline. Dystrophic waters show much the same oxygen relations as do eutrophic ones, although here it is the presence of strong reducing substances in the allochthonous detritus rather than appreciable bacterial action that accounts for the oxygen consumption in the hypolimnion (63).

The oxygen relations are not, however, always quite as diagrammatic. Thienemann (135, p. 384) already draws attention to the case of Green Lake examined by Birge and Juday (9, p. 46) which, although oligotrophic, shows a slightly increased oxygen consumption for some little distance above the bottom and he cites the lake of Davos as another example of the same phenomenon. Werestschagin (157, p. 238), moreover, describes for Lake Segosero (97 metres deep) a maximum oxygen content in summer at between 50 and 80 metres depth, whilst both towards the surface and the bottom there is a decrease in the percentage of oxygen, and he points out that there are indications that similar features occur in other deep lakes.





Oligotrophic (Seneca Lake, New York, 3. viii. 1910)



Eutrophic (Grosser Plöner See, 15. viii. 1916)

FIG. 1. Comparison of temperature and oxygen content at different depths in oligotrophic and eutrophic waters. (From Thienemann, *Binnengewässer*.)



With reference to the current explanation for the marked horizontal oxygen stratification observable in deeper waters and in particular of the pronounced oxygen deficiency in the hypolimnion of eutrophic waters, it must be pointed out that we have at present no data as to the rate at which the diverse constituents of the plankton sink through the water and consequently of the length of time during which any given plankton form remains suspended in the waters of the hypolimnion. Moreover, we have as yet little information about the processes of bacterial decay in the deeper strata of the water or, for that matter, of the actual Bacteria that are at work or of their conditions of existence and operation (cf. however 26, 130, p. 334; also 68 *a* and the other literature cited there). It may well be that the amount of decay in the hypolimnion will depend materially on the type of plankton and on the special conditions obtaining in each piece of water accelerating or retarding decay. The fact that in many cases examination of the sediments shows the persistence of plankton organisms in a more or less recognisable form (98, 153) lends support to the view that sometimes at least there may be little decomposition until the bottom is reached.

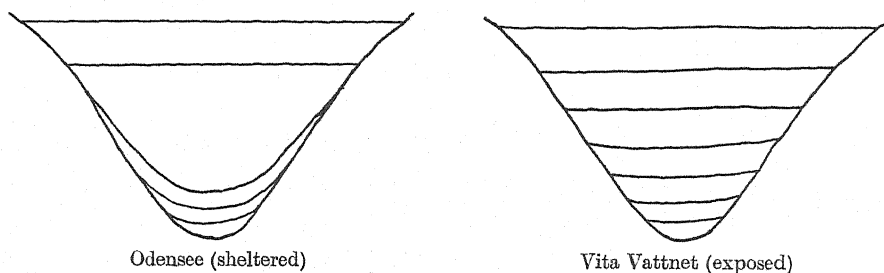


FIG. 2. Comparison of oxygen stratification in a sheltered and in an exposed lake (after Alsterberg).

Alsterberg (5, 6) has shown that, apart from the macro-stratification, there exists a micro-stratification immediately above the bottom, conditioned by the processes of decay proceeding there. He has demonstrated (5, p. 264) that, in a lake that is sheltered from winds, the oxygen stratification in the hypolimnion is not horizontal, but closely follows the configuration of the bottom (Fig. 2, left-hand diagram), and he ascribes the horizontal stratification usually observed (Fig. 2, right-hand diagram) to the mixing effect of winds and to currents set up by unequal heating of different parts of the water. These are conditioned by absorption of heat by the layers of water immediately overlying the sediments (6, p. 6) which constitute a reservoir of heat (cf. also 11). Alsterberg is of the opinion (cf. 5, p. 273) that the decay of the sinking plankton has little to do with the oxygen stratification, and Lundberg (65, p. 384) specially emphasises the fact that in most pieces of water the plankton will become sedimented at different levels, so that in the shallower regions at least it will certainly not undergo decay before reaching

the bottom. Nevertheless, these two investigators do not appear to have proved conclusively that there is not an appreciable amount of decay on the part of the plankton in deeper waters before it reaches the bottom and that these processes may not play a considerable rôle in conditioning the oxygen stratification. Their work is, however, of great value because it has drawn attention to the importance of considering the bottom configuration in this connection and such considerations may explain some of the anomalous cases previously referred to (p. 238). Lundberg's statement that decay must also take place more slowly in the colder waters of the hypolimnion remains to be proved; American workers (26, p. 377; 29 a) have shown that many of the fresh-water Bacteria operate as actively at lower as at higher temperatures.

Returning once again to the three types of waters distinguished by Thienemann and Naumann, it may be added that oligotrophic lakes are in general deeper, with a comparatively narrow littoral shelf and scanty littoral vegetation and a more extensive hypolimnion as compared with the eutrophic type, while the dystrophic are variable in depth, but practically always possess scanty littoral vegetation<sup>1</sup>. The extent of the littoral zone is a factor of great importance, since its shallow waters are readily warmed and often show a high degree of productivity whose surplus becomes available to the lake or pool as a whole. Thienemann (140, p. (87)), speaking of the Central European lakes, points out that, as a general rule, those having an average depth of 18 metres or more are oligotrophic, while those of a lesser depth are eutrophic. This would justify the view that the character of a lake is determined largely by the form of its basin, and Thienemann goes so far as to suggest that, if this correspondence does not obtain, artificial alteration of the character of the lake is always to be suspected. Many other investigators have commented on the richness of the plankton in shallow waters (cf. 12, p. 35; 48, p. 185), and Naumann (84, p. 646) has pointed out that under uniform geological conditions plankton productivity is in the main indirectly proportional to the depth.

In establishing the main types too much stress has probably been laid on the concept of a lake as a practically self-contained microcosm, shut off from most foreign contamination, so that the characteristics are largely determined by geomorphic features. Since the latter often fall into line with the character of the immediate environment (150), their importance has perhaps been overestimated. But in the majority of cases there are inflowing streams (cf. 116) and the presence of woods or artificial plantations in the neighbourhood, as well as of more or less extensive tracts of cultivated ground, will greatly heighten the relative effect of outside influences in relation to the primary geomorphic features (131, p. 122). Decksbach (21, p. 278) draws special attention to the seasonal operation of natural factors, such as great floods

<sup>1</sup> With reference to the general biological relations and the nutritive cycle in lakes, with which it is not possible to deal here, cf. especially 4, 130, 139.

and the transport of sand by wind, leading to mineral sedimentation far beyond the realms of the littoral zone to which such deposits are usually restricted.

Donat (28), moreover, has distinguished two types of oligotrophic waters, namely those which are conditioned by geomorphic causes and those which are determined largely by physiological causes, in other words by the scanty mineral content of the water. He points out that the majority of North German waters showing oligotrophic characters possess a vegetation that is only to be distinguished quantitatively from that of the eutrophic type (cf. also 81, p. 15). Such have a narrow marginal ledge (the U-shaped type of Ström, 131, p. 117), so that the *Phragmites* zone and other littoral macrophytes can only achieve a scanty development. The low plankton productivity of such waters is attributed to the prevailing low temperature of the water owing to the absence of a broad, shallow, readily warmed littoral zone. It is suggested that the available salts cannot be exploited by the littoral vegetation owing to the lack of room and by the phytoplankton owing to the low temperature, and it is indicated that the majority of subalpine lakes probably belong to this type<sup>1</sup>. It may perhaps be doubted whether the low plankton productivity of Donat's geomorphic type is correctly ascribed to the low temperature, since Schiller (119) has recently shown that cold water (11–12° C.) is often more productive than warm (23–25° C.). A more probable explanation may lie in the scanty littoral zone and the resulting restricted breeding ground for the plankton (cf. p. 244). Another good example of the geomorphic oligotrophic type is seen in Lake Hurdals in Norway (39).

Donat's second, the physiologically oligotrophic type, specially studied by him in Pomerania, is distinguished by the absence of *Phragmites* and *Potamogeton*, the presence of *Lobelia* and *Isoetes* (always also the liverwort *Aneura sinuata* var. *submersa*), and the occurrence of a Desmid plankton which is poor in number of individuals.

It appears to me that here we are able to establish contact between the continental work and that done on the waters of the Lake District. The lakes with Desmid plankton correspond to Donat's physiologically oligotrophic type, while those with a plankton of Diatoms and Myxophyceae represent a step in the direction of his geomorphic oligotrophic type. The point of greatest interest lies in the fact that Pearsall has undoubtedly established a transition between the two types (cf. especially 104, p. 275) which, if I interpret Donat rightly, he does not believe to occur in the district investigated by him. It can hardly be doubted that the geomorphic oligotrophic type would in its further evolution pass over to the eutrophic type. In fact it would seem that the Lake District is peculiarly favourable for the study of incipient eutrophy and the changes that go hand in hand with it. A study of the thermal and oxygen relations and of the bottom sediments, especially in relation to the fauna, is much to be desired.

<sup>1</sup> Whether Naumann's ultra-oligotrophic type (85, p. 101) belongs here is not altogether clear.

That the oligotrophic type can pass over into the eutrophic has of course long been known, and neither Naumann nor Thienemann have failed to recognise the existence of manifold transitions<sup>1</sup>. The classical case is that of the lake of Zurich where, following on the discharge into the lake of the sewage effluent, an entire alteration of its character took place (29; 71; 72, p. 148 *et seq.*; 73); another example that has been studied in detail is that of the Hallwilersee (16)<sup>2</sup>. In such cases artificial factors have been at work (cf. also 85, p. 104), but eutrophy can also result from the operation of natural factors (58; 138, p. 210; 166, p. 264; 167). The suggestion of a development in the converse direction, from eutrophic to oligotrophic, has been made by Gams (34, p. 125; cf. also 129, p. 109). Cases are also on record of the passage of oligotrophic to dystrophic types (140, p. (87)), and Decksbach (24) gives for Russian lakes a possible transition between the two via an eutrophic stage (cf. also 33, p. 290). It is of course also to be expected that, under certain conditions, only part of an oligotrophic basin will undergo change to an eutrophic character; some parts of the Lake of Lugano belong to the one, others to the second type (29, p. 21; 138, p. 210; cf. also 23, p. 499; and 158).

While there are thus evidently many variants of the two (or three) main types and these are linked up in various ways by transitions, the primary distinction of lake waters into oligotrophic, eutrophic and dystrophic types is a most valuable one, since it is based not on one factor only, but on practically the whole complex, physical, physiological, and biological. There can be no doubt, however, that these distinctions are not applicable solely to the larger basins, but apply to all bodies of standing water (85, p. 102; 86, p. 655). Lake, pool and pond are but entities of different dimensions, and a classification of aquatic communities as amongst these three is altogether impossible (91, pp. 1, 13). There are shallow lakes and deep ponds and any rigid definition is out of the question. This is clearly indicated *inter alia* by the results arrived at by Griffiths (41), although his data are not adequate for a full elucidation of the matter. The deep rocky pools with little phanerogamic vegetation and scanty phytoplankton are clearly oligotrophic in character, while the shallow weedy ones are eutrophic. One would like to have some exact data as to the oxygen relations and bottom sediments of these various pools and ponds, and I am inclined to think that the investigation of these matters in the deeper rocky pools with little organic life would not support Dr Griffiths' view of the oxygen deficiency in the lower strata of the water. Continental work has shown that such oxygen deficiency only exists where there are

<sup>1</sup> Lundbeck (64, p. 329) distinguishes five different communities of bottom fauna in the passage from oligotrophy to eutrophy. With reference to the effect of increased mineral nutriment on plankton productivity, see 52 and 76.

<sup>2</sup> With respect to the eutrophy of ponds, cf. 118. Gams (33, p. 292) states that *Anabaena flos aquae* is now a regular constituent of the plankton of the Lake of Constance, while Schröter and Kirchner in 1896 (122, p. 27) mention the entire absence of Myxophyceae.

copious organic sediments undergoing decay and presumably that is not the case in the pools in question.

Nordqvist (99, pp. 80, 87) does maintain a distinction between puddles, ponds, and lakes, since he finds that many zooplankton forms found in puddles are not to be met with in ponds and that forms characteristic of the latter do not occur in lakes. A perusal of his lists shows, however, that the zooplankton of ponds comprises forms met with in puddles and others met with in lakes, so that the difference is evidently only one of degree, and it is to be expected that all kinds of connecting links will be found. The same is no doubt true of the phytoplankton.

The shallowness of many pools and ponds, however, introduces a factor that does not come into operation in deeper waters. In these latter there must, with few exceptions (cf. 125 *a*, p. 24), be thermal stratification (cf. also 151 *a*), so that the water of the hypolimnion is cut off from the surface waters except at the time of the vernal and autumnal circulations. The products of decay of the bottom sediments are therefore locked up in the lower layers and only become available to the life of the lake as a whole when the whole-volume circulation takes place; moreover, in the eutrophic type, many of the processes of decay in the bottom sediments will tend to be anaerobic. In the case of a pool or pond only a few feet deep, however, every strong wind (unless the piece of water be especially sheltered) will bring about a whole volume circulation, the water will tend to be well aerated throughout and, even with rich organic sediments, the processes of decay will be prevalently aerobic. It is clear that such conditions are specially favourable to the development of many Volvocales and Chlorococcales (cf. 41, p. 208) amongst others, and that this accounts for their prevalence in smaller shallower pieces of water (cf. also 171).

In this connection it may be noticed that the same conditions obtain over the shallow marginal shelf<sup>1</sup> bearing a growth of macrophytes, that develops in most pieces of deeper water at an earlier or later stage in their geological history. Here too, there will be adequate oxygenation owing to wind action and decay of the shallow-lying sediments will be aerobic, so that here also green unicellular and colonial and other shallow-water forms will find ideal conditions for their development. And from this marginal fringe they will extend into the plankton over the deeper water and be the more abundant the more extensively the marginal fringe is developed (cf. 84, p. 647; 86, p. 658). The point that has just been brought out may be stated in another way, viz. that in a shallow pool or pond the marginal shelf of the deeper piece of water extends over the whole area, and the significance of this fact, though it has often been stated, has perhaps scarcely been clearly realised. It means

<sup>1</sup> Such shallow waters (especially on the northern banks) may often attain to high temperatures in the early spring (cf. 3; 155) which may be of great importance for the rapid development of the littoral plankton community.



that the aquatic communities of the pond or pool are to be compared with those of the lake margin.

This immediately raises the question of the status of the plankton. I do not believe that we shall ever arrive at a clear conception of plankton, until we know where it comes from. It will be a familiar fact that the phytoplankton usually shows a very marked periodicity, phase succeeds phase often within a relatively short space of time, and in any month a form that was previously abundant may have as good as disappeared. What becomes of the resting stages or persisting individuals that give rise to the fresh burst in the next season? In many of these forms no spores or cysts are known (very notably so in the case of the Desmids), so that the cycle is presumably carried on by a few persisting individuals. Where are they? I strongly suspect that they are to be found in two places, at the bottom and in the littoral zone.

There is no reason to refuse to accord the name of plankton to the free-floating element (heleoplankton of Zacharias, 170) of a shallow pond or pool, and there is equally little justification to withhold the name from the free-floating element in the shallow littoral zone of a larger and deeper piece of water. The two are certainly similar in character and will often be found to differ very markedly from that over the deeper water in the central region of a lake, although mixing will no doubt occur more or less readily. Naumann (82, p. 101; cf. also 8, p. 125) distinguishes between littoral and pelagic zones as regards the plankton, and I believe it will be very profitable to differentiate between littoral plankton<sup>1</sup> (the benthoplankton of Griffiths, 41, p. 209) and pelagic plankton (the eulimnetic plankton of Apstein and Schröter and Kirchner, 122, p. 14; limnoplankton of Griffiths), the latter being that occurring over the deeper water where macrophytic growth is lacking. I suspect that the majority, if not all, of the typical constituents of the pelagic plankton are to be found at the bottom during their period of absence (in this connection, cf. especially 12, pp. 10, 38), which does not of course rule out their simultaneous occurrence in the littoral zone. Wesenberg-Lund (154 a, p. 418) has expressed the opinion that the new phases arise from resting stages deposited in the shallower water near the shore and that those which sink to the bottom in the deeper water sooner or later perish. If this be true, then in lakes possessing only a narrow marginal shelf the opportunities for a yearly renewal would be very small. But the great power of resisting adverse conditions established for the resting stages of many algae renders it probable that even when they sink in deeper water, some may subsequently germinate and again reach the surface.

<sup>1</sup> I would comprise as littoral planktons only those organisms which are normally free-floating during the whole or part of their existence and which are capable of multiplication as free-floating forms. The term is therefore not altogether synonymous with the bathylimnetic plankton of Schröter and Kirchner (122, p. 14) which seems to me to include both littoral and tycholimnetic elements (cf. also 165, p. 53).



The degree of adulteration of the pelagic with littoral plankton will depend on the quantity of the latter (which will be dependent on the extent of the littoral shelf) and the facilities for its distribution into the open water; moreover, multiplication of the littoral planktons in the open water will naturally only take place if the latter contains an adequate amount of mineral nutriment. Naumann (90, p. 15) points out that *Scenedesmus quadricauda* does not figure in the pelagic plankton of oligotrophic waters, although often abundant in that of eutrophic waters. It is, however, present in the littoral zone of the former, but the paucity of nutritive salts does not admit of its obtaining a foothold in the pelagic region. From the point of view that has just been put forward, it is much to be desired that experiments on the rate of drift at different times of the year and from different parts of the shore line, both towards the open water and *vice versa*, should be undertaken on a number of the larger lakes (cf. 154 a, p. 430; 164, p. 56). They would probably help to explain many peculiar and variable features of the plankton, and the conjecture may be hazarded that the change from the oligotrophic to the eutrophic types is in the first place largely due to an increasing adulteration of the plankton by the littoral supply. Localised distribution of the Algae in a piece of water has been recorded by several investigators (8, p. 698; 41; 47, p. 163; 48, p. 149; 57; 156; 157, p. 241).

Griffiths (43; cf. also 48, p. 175; 126, p. 40) has propounded the view that the Desmid plankton previously discussed is composed of forms that occur so scantily in the littoral zone and in the adjacent terrain that they are likely to be overlooked there, but that they find better conditions of existence and multiplication in the open waters of the pelagic region when carried into them; as an alternative hypothesis he suggests that they may survive in the pelagic region in a modified form. It is, however, not clear whether he believes that this happens each year. Pearsall (106, p. 64) has already stated that some of the plankton Desmids are carried out from the littoral zone through wave action and currents caused by wind, while Wesenberg-Lund states that the plankton Diatoms are derived from the bottom and the shore (154, p. 15).

In a shallow pool or pond the littoral plankton is alone present, although naturally there will be differences of degree and in certain shallow waters some of the pelagic forms will also be found. In general, however, such pelagic planktons will be those capable of tiding over a period of existence in deep water where photosynthesis cannot occur or will at least be at a minimum. It is quite possible that there are only relatively few of them. Why the majority of them do not commonly occur in shallow waters is at present in most cases not apparent. Dr Griffiths finds that *Ceratium hirundinella* and *Asterionella* occur only in deep pools in which stagnation conditions obtain (41, p. 204) and ascribes this to the presence of sediments lying in a region poor in oxygen. As already mentioned, I do not think that there is good evidence that this explanation is correct. Naumann (87, p. 57) states for the

ponds of Aneboda that the poorer the water in mineral salts, the more does the phytoplankton approximate to that of lakes, whilst the richer the water, the more does the plankton have the character typical of that of ponds, which would seem to indicate that it is richness in nutritive material that rules out the typical pelagic planktonts.

The primary distinction of waters into oligotrophic, eutrophic and dystrophic types affords a classification which is capable of further development. In this connection Naumann (81) has elaborated a concept of so-called environmental spectra (Milieuspektra), distinguishing for each factor (nutritive salts, detritus, dissolved gases, temperature, light and later (89) pH) three grades, the oligotrophic, mesotrophic and polytrophic grades, based upon the intensity with which it is represented. In many cases these distinctions are at present largely theoretical and it may be doubted whether it is necessary to have a cumbersome terminology in order to make the effect of the different intensity of each factor clear. It is of course apparent that, as regards the spectra of nutritive salts and detritus, waters will in general depend on the geological formation in which they lie, and this is the basis of the concept of a regional classification of waters that has been specially elaborated by Naumann (81, 85, 92, 95). In this connection a distinction of primary importance lies in the calcareous or non-calcareous character of the environment, as has long been recognised. Thus, already in 1899, G. S. West (159, p. 50) comments on the paucity of Algae in the chalk districts of Cambridgeshire, and it is a familiar fact that but very few Desmids are to be found in calcareous waters. Schmidle (120, p. 68) and Rabanus (112, pp. 24, 76) have likewise drawn attention to the marked contrast between the calcareous and non-calcareous waters of the plain of the Rhine (cf. also 59, p. 74).

Recently Naumann (97) distinguishes the following variants of the oligotrophic type: (a) the harmonious oligotrophic facies with all spectra of the oligotrophic type, easily passing over into the dystrophic; (b) the acidotrophic facies; (c) the dystrophic facies; (d) the alkalitrophic facies, with bottom deposits rich in calcareous matter; (e) the siderotrophic facies, with bottom deposits rich in iron (cf. also 93); and (f) the argillotrophic facies, rich in suspended clay. It is stated that these types may be pure, but that combinations often occur; thus eutrophy is often combined with argillotrophy, especially in the fertile Baltic plains situated on clay. In an earlier communication (81, p. 12) the eutrophic type is distinguished into (a) the ortho-eutrophic facies with a medium calcium content, (b) the gypso-eutrophic facies with a high percentage of calcium, and (c) the para-eutrophic facies, in which the eutrophic character results from detritus, etc. introduced from outside (Humusschlammseen of Utermöhl? cf. p. 237 and 129, p. 103). Ström (129), who gives a slightly different classification, suggests that the large and deep Scottish lochs (cf. 154 a, p. 410) possibly represent a special facies of the para-oligotrophic (dystrophic) type; these have yellowish brown waters rich

in humic substances, although probably possessing only a low oxygen consumption, and have a rather high calcium content. Similar lakes are stated to occur in Rügen. It is not possible to go into further details respecting the classification of waters (cf. also 33), the more so as many of the types distinguished are as yet very superficially known, the distinction of many being at present based on a single factor.

While the fundamental distinction of lake types and of other types of natural waters has materially contributed towards a general understanding of the basis of algal ecology, we are still in most cases as ignorant as ever of the determining factors for the distribution of individual species, nor do we possess the means in most cases to distinguish the numerous algal communities that are to be found in diverse waters, as well as in different parts of the same water. Many investigators have published lists of species that appear to represent distinctive communities, but it may be pointed out that such communities require to be causally related to their habitat before they can be accepted as ecological units.

Various attempts have been made to determine the influence of hydrogen-ion concentration, which varies appreciably in different kinds of waters<sup>1</sup>, on the distribution of algal species<sup>2</sup>, but it can hardly be said that they have taught us much more than was already previously known. Wehrle (152, p. 221) distinguishes four categories of waters: the very acid, the moderately acid which sometimes show slight pH variations, the permanently alkaline (calcareous) waters, and lastly those in which there is in summer an almost diurnal variation between an alkaline and a moderately acid reaction, the demonstration of the existence of these last being perhaps his most important contribution (cf. however 61, 117); the variation is usually much more pronounced in the surface than in the lower layers. The content of soluble inorganic salts runs practically parallel with the pH, being lowest in very acid and highest in very alkaline waters. The greatest abundance of species was found in the moderately acid waters. The largest number of species strictly limited to water of a given type occurred in the strongly acid waters, whilst the smallest number was found in the alkaline waters. But practically all these facts had been established without pH determinations and Wehrle's results are only corroborative of what was previously known. Thus, Magdeburg (68, p. 164) had already shown that in the manifold algal flora of moorlands, there occur a limited number of sphagnophilous species (largely Desmids)<sup>3</sup>

<sup>1</sup> Strøm (127) gives average pH values for a number of different habitats in the Norwegian mountains.

<sup>2</sup> A useful oversight of hydrogen-ion concentration in relation to aquatic biology is given by Bresslau (15), who also (p. 72 *et seq.*) summarises the knowledge to date with respect to the influence of plants on the pH of the water (cf. also 69).

<sup>3</sup> The species in question are: *Eunotia exigua* (Bréb.) Rabenh., *Navicula subtilissima* Cleve and var. *minor* Magdeb., *Penium oblongum* (de Bary) Lütkem., *P. minutum* (Ralfs) Cl., *P. polymorphum* Perty, *Cosmarium cucurbita* Bréb., *C. pygmaeum* Arch., *Euastrum binale* forma gut-

which are the only ones to be found in those waters which are completely shut off from the underlying rock by a layer of peat. These forms appear to be the only ones able to exist under the special conditions that obtain in these waters, viz. poverty of mineral salts, strong acid reaction, relatively low temperatures, and the presence of humic acids. It seems clearly established that they constitute a definite algal community characteristic of such waters in many parts at least of the north temperate zone. Similarly the work of Schmidle, Rabanus, and others had plainly demonstrated that only very few species were distinctive of alkaline waters.

Wehrle epitomises in a table for all the species observed by him the range of  $pH$  over which they were found. With reference to this table two things are to be noted. With very few exceptions the species that are recorded as having a very limited  $pH$  range were only found in one or in a very small number of localities. Ström (128) has also determined the  $pH$  of the waters in which the species recorded by him occurred. Where the two investigators found the same species and Ström found it more widely than Wehrle, he nearly always extends its  $pH$  range and *vice versa*. The impression that one obtains is that, if a sufficiently extensive range of habitats be examined, the majority of algal species will be found to exist under a wide range of hydrogen-ion concentration. This does not mean, however, that the  $pH$  has no influence on algal distribution. It is more than probable that, while most fresh-water Algae are tolerant of a wide range of hydrogen-ion concentration, their optimal development may take place only within a limited range.

In this connection reference may be made to the interesting experiments described by Skadowsky (124, p. 129). Collections of plankton, from which the larger forms had been removed by filtration, were placed in the natural pond water, whose  $pH$  was varied by the addition of caustic soda and sulphuric acid respectively. The diverse cultures were exposed to identical conditions of temperature and illumination, and the number of individuals of each species present in a given volume was subsequently estimated. The results (Fig. 3) showed that a maximum development of several species occurred only at a definite hydrogen-ion concentration, although more or less considerable numbers were to be found at ranges above and below the optimum. Others, however, such as *Menoidium semilunare* (Euglenineae), showed an abundant development over a wide range of  $pH$ , so that stenoionic and euryionic types can be distinguished. It can hardly be doubted that these results are of wide application and that a large number of Algae will be found to attain abundance only within relatively narrow ranges of  $pH$  (cf. also 89, p. 298), although they may occur in smaller numbers within a much wider range.

*winckii* Schmidle, *Arthrodesmus incus* var. *minor* West, *Staurastrum margaritaceum* (Ehrenb.) Menegh., *S. polymorphum* Bréb., *S. nigrae-silvae* Schmidle, *S. furcatum* (Ehrenb.) Bréb., *S. monticulosum* var. *bifarium* Nordst., *Tetmemorus brebissonii* (Menegh.) Ralfs, *Gymnozyga brebissonii* Wille, *Oedogonium itzigsohnii* De Bary, *Oocystis solitaria* Wittr. vars. *elongata* Printz and *asymmetrica* (West) Printz, *Anabaena augstumalis* Schmidle.

If pH determinations were made only in relation to species that showed a great quantitative development, more informative data might be obtained.

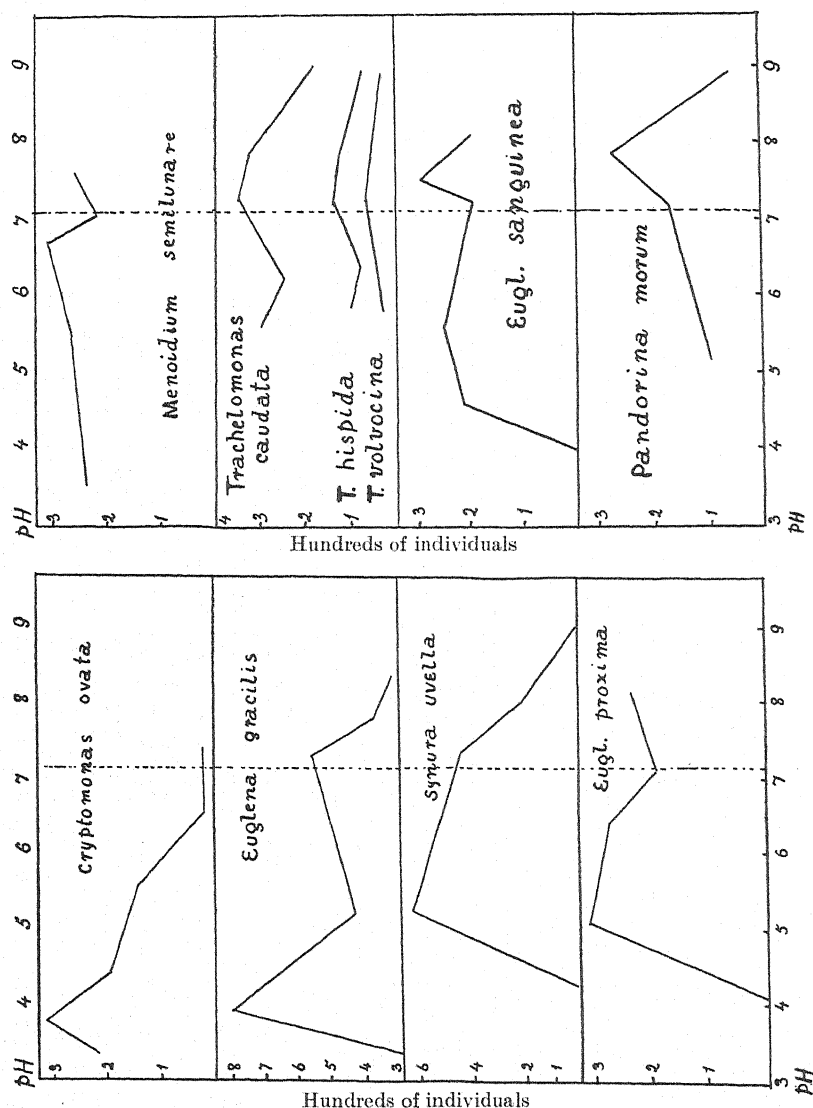


FIG. 3. Curves showing frequency of various organisms at different hydrogen-ion concentrations (after Skadowsky).

It would also be useful to know how far the termination of the period of abundance of a given form coincided with a change of pH<sup>1</sup>. There is no doubt

<sup>1</sup> According to Ulehla (143, p. (23)) growth of *Cladophora* is greatest at a pH of 7.7-7.9, but ceases at 7.2, at which zoospore-formation occurs. The growth-optimum for *Spirogyra* is at 7.2, whilst at 7.7-7.9 zygote-formation commences.



that a sudden alteration of the  $pH$  is disastrous to a large number of forms. Sebenzow (123) describes how a change from  $pH$  6 to  $pH$  2 killed most of the animal organisms present, the larvae of *Anopheles maculipennis* disappearing completely. The Algae (*Ankistrodesmus falcatus*, a few Desmids, Diatoms, and Flagellata) showed a greater power of survival, but were strongly diminished in numbers.

The  $pH$  toleration of fresh-water Algae may, moreover, vary with climatic conditions and with other factors of the environment, and in this connection it is to be noted that Skadowsky's experiments were carried out under constant conditions. The effect of other factors may explain certain marked discrepancies. Thus Tannreuther (132, p. 380) states that *Euglena gracilis* only grows well in an alkaline medium, whilst Skadowsky (*loc. cit.*) gives for the same species an optimum  $pH$  at just below 4.

Unfortunately a considerable amount of the experimental work on hydrogen-ion concentration in relation to Algae is of little value owing to the absence of specific determinations. To make generalised statements with reference to such large genera as *Euglena*, *Spirogyra*, *Oedogonium*, etc. is absurd, as the numerous species certainly differ among one another in their  $pH$  relations. Cowles and Schwitalla (20) give the optimum  $pH$  for an unnamed *Euglena* as 6.5, but the work of Skadowsky shows that different species of this genus have very different optimal  $pH$  concentrations.

The work of Ulehla (143, 144) is open to the same criticism. It is improbable that the relatively narrow range of  $pH$  values given for *Spirogyra* and *Oedogonium* can apply to all or even the majority of the species of these genera. It is of course a familiar fact that their species are not usually found in markedly acid waters, although *Oedogonium itzigsohnii* is a member of the special moorland community distinguished by Magdeburg (68, p. 167). But quite apart from this, species of the two genera under discussion are to be met with in very varied types of waters and many are common in small collections of water where there must often be a considerable diurnal  $pH$  range. Ulehla (143, p. (26)) accounts for the occasional occurrence of species outside the normal range as due to the possession by these species of an incrustation of calcium and iron carbonates formed by epiphytic bacteria and constituting a local buffer system, which renders the alga independent of the reaction of the water. This is regarded as a type of symbiosis, and it is suggested that such living buffer systems may be widespread. A more careful investigation is necessary before the value of this suggestion can be estimated (*cf.* 146, p. 90).

Gams (33, p. 290) points out that the ubiquitous plankton alga *Botryococcus braunii*, which is to be met with in many diverse kinds of waters, shows characteristic variations according to their reaction. In oligotrophic lakes it is found only as the large green form; in smaller bodies of water rich in humus, but poor in nutriment, it is represented by a small brown form, while in waters



rich in nutriment it always occurs in the red form. In mesotrophic waters; the red form dominates in winter, the green form in summer. It is likely that other examples of such special habitat forms will come to light.

With reference to the principal categories of waters previously distinguished, Naumann (89, p. 302) emphasises that neither in oligotrophic nor in eutrophic lakes are any marked extremes of hydrogen-ion concentration to be observed, so that the conditions admit of the development of a large diversity of organisms and other factors than the *pH* determine the quality of the phytoplankton (and no doubt of the algal flora generally). In eutrophic lakes, however, there is a marked difference of *pH* between the upper and the lower layers of the water (12, p. 34). According to Skadowsky (124, p. 114) also the *pH* is very constant in deep lakes with hard waters and in acid waters. He points out that in eutrophic waters the variations in *pH* are the greater, the smaller the concentration of dissolved salts and the shallower they are, and both he and Naumann (89, p. 302) ascribe this to the high plankton productivity. The influence of the latter on the reaction of the water evidently varies with its nature, the highest degree of alkalinity being produced by a Myxophyceous plankton.

At this point attention may be drawn to the work of Uspenski (145, 146) which indicates that the iron content of the water may be a limiting factor. For a considerable number of Algae (cf. also 147, p. 273 *et seq.*) he was able to establish that normal growth only occurs between concentrations of 0.2 and 2 mg. of ferric oxide per litre, while in natural waters these limits are sometimes exceeded; the iron concentration, moreover, varies with the time of the year and with meteorological conditions and other factors. Since, with increasing acidity, more iron compounds will be dissolved out of the substratum, the *pH* of the water determines the amount of ionised iron present; Skadowsky (124, p. 138) mentions that with a *pH* of 8.8 only traces of iron in its active form will occur in the water. In moorland waters, however, the abundant organic compounds present act as buffers. According to Uspenski (146, p. 29; cf. also under 124, p. 144) *Cladophora* can be grown in water having a *pH* of 6.7 for months, if the nutritive solution is made up with a smaller quantity of iron than in the normal solution, since in the more acid water the iron is more completely ionised. This has a marked bearing on Uehla's work discussed above, as well as on other *pH* investigations, and indicates that some of the results ascribed to a change of *pH* may actually be due to a change in iron content. The forms that are most resistant to a high concentration of iron (Diatoms, *Vaucheria*, Heterokontae) are those which do not store starch and which possess an acid protoplasm. Uspenski enumerates (p. 55) a number of forms that can be used to estimate the iron content of the water in which they occur. According to him this factor is of most importance in determining the vegetation of streams and moorland waters.

At an earlier point attention was drawn to the fact that the algal vegetation of shallow ponds and pools lives under conditions which are very analogous at least to those obtaining over the littoral shelf of the larger and deeper lakes. A closer comparison between the two than has hitherto been undertaken would probably prove of interest. Certain differences are of course to be expected, but these should be given precision; they will depend on differences in substratum, on greater degree of movement of the water, and above all on the probable influence of the neighbouring deep water on the littoral zone. Relatively little work has, however, so far been carried out on the littoral algal flora of lakes and, apart from disclosing the general similarity to that of ponds and shallow pools, it has not with few exceptions to be mentioned later contributed much to the furtherance of our knowledge of algal ecology.

Before turning to consider the littoral zone of a lake, however, a few words may be said about the algal flora of ponds. As will be familiar, this is often very rich, comprising representatives of all classes and families of Algae and, above all, it is bewildering in its manifold character. I do not suppose that it would be possible to find two ponds in which the algal flora is the same, and it is a well-known fact that neighbouring ponds, situated in the same geological substratum and apparently identical in character, may nevertheless harbour a very distinctive algal flora, especially as regards the unicellular and colonial forms (cf. also 86, p. 659).

Ponds are at least largely of the nature of islands. Where there is no definite inflow, their algal population must reach them from without, so that a considerable element of chance (102) becomes a factor in determining their flora. Even when fed by a stream, this will introduce only those forms which it itself harbours. Distribution of fresh-water Algae can be effected in two ways, viz. by wind or by animal agency (wading birds and insects, 70). Dried mud, containing resting spores or merely dormant individuals, if blown away by the wind may on reaching a suitable piece of water lead to the establishment there of the forms thus conveyed. Similarly Algae may no doubt be distributed in the mud clinging to the feet of wading birds or by water-beetles and the like. The relative efficacy of these two methods is not yet known, but the successful establishment of an algal form in a piece of water will not depend only on the character of the latter, but also on the period of its introduction. As Naumann has pointed out (86, pp. 667, 670), a slight infection (i.e. introduction of but a small quantity of spores or individuals) can in all probability only be successful if the microscopic fauna is temporarily at a minimum. He makes this point with special reference to the plankton, but it may well be of wider application.

Naumann (86) lays emphasis on the fact that the artificial ponds of the Botanic Gardens at Lund, which are of the eutrophic type, have during a period of observation of fifteen years only shown the establishment of one

foreign plankton alga—*Lyngbya contorta* Lemm. (cf. also 87). Direct attempts to introduce foreign plankton forms were without any success. It seems probable that such data are applicable to a large part of the algal flora and especially to those forms which do not readily form spores. The Desmids, which West (161, p. 428) lists as fairly generally distributed in ponds and ditches in temperate countries, are all forms producing zygospores and most of them forms in which zygospore production is an abundant phenomenon. It seems probable therefore that, except in a long-established pond, many forms will be lacking that could exist there. Moreover, some of the forms which are present may occupy a position of greater prominence than would be the case if they were subjected to the competition of others that could (and perhaps would at a later stage) establish themselves there. And this of course must apply to the whole potential population of the pond, plants and animals alike. It seems that many Crustacea and insect larvae will devour any Algae that are available, while others like many Rotifers and the Ephemerid larvae exercise some degree of selection (cf. in this connection 36; 40; 47 a; 78; 79; 80; 109 a, p. 310 and the other literature there cited; 125 a, p. 146 *et seq.*; 168)<sup>1</sup>. The character of the fauna may therefore be of considerable importance in relation to the question of the gradual colonisation of a piece of water.

The previous considerations indicate that the climax in a body of water may require a very long time for its achievement, a period that is perhaps to be reckoned in hundreds of years. It is therefore only in old-established waters that one can expect to find a complete balance between the biotic communities, and for this reason lakes and large pools will afford better material for the study of algal communities than small ponds. Any attempt at classifying the latter should be based rather on the forms which are present, since absence may merely imply that the forms in question have not yet had the opportunity to become established.

There is, however, one important source of infection from which colonisation of a piece of water may ensue, viz. as a result of drainage from the algal flora of the adjacent soil, a method possibly available only when the surrounding land is cultivated. Recent work (17, 74) has shown that cultivated soils harbour a very great diversity of algal forms, especially of unicellular and colonial types. Some are definitely restricted to the soil, but many are aquatic types (cf. especially 51). Whether uncultivated soils are similarly rich is at present unknown. A comparison of the soil algal flora with that of ponds situated amid the soil in question would be of interest. But another aspect lies in the source of this manifold algal life that can be obtained from soil cultures. It is hardly to be supposed that the soil is the natural medium for a large number of the forms involved, and one is tempted to believe that their

<sup>1</sup> Naumann and others have shown, however, that the fine organic detritus constitutes the chief nutriment of many zooplankton forms (cf. especially 78).

presence there is to be explained as the result of wind or animal dispersal of spores or dormant individuals which, failing to reach a piece of water, remain there in a resting condition or, possibly in cultivated soils, in part find favourable conditions for growth and multiplication.

We may now turn to a consideration of what is known with respect to the littoral algal communities of lakes, in the course of which, however, occasional references to observations on smaller pieces of water will be included. The most complicated features are to be found in the shallow littoral zone where the largest number of forms occur and competition is keen. As we pass out into the deeper water and the multiplicity of substrata becomes lessened, the all-important effect of the decrease in light intensity (possibly in conjunction with increasing oxygen deficiency) becomes marked and distinctive communities are more easily recognised. In the shallow littoral zone all manner of substrata, organic and inorganic, dead and alive, are peopled with an abundance of epiphytes and sessile animal forms. Many of the former are permanently epiphytic, unless torn off from their substrata by wave action. Others are only temporary epiphytes, such as the species of *Diatoma* and *Tabellaria*, which after detachment are capable of existence as plankton forms when the form of the colony changes from a chain to a star (154, p. 19).

It must, moreover, be realised that a very large proportion of the Algae of the littoral zone and of other shallow waters are epiphytic in the first stages of their growth, namely nearly all those that originate from zoospores, such as *Cladophora*, *Oedogonium*, *Ulothrix*, *Tribonema*, etc. Their early growth is thus conditioned by the presence of available substrata and by competition with the numerous other epiphytes (165, p. 51). Such forms contrast with the Zygnemales, for example, which mostly arise from unattached stages (zygospores or possibly fragments) buried in the mud. Many of the zoosporic forms can, however, also propagate by unattached aplanospores, akinetes, and the like, so that they can be included under two biological categories. This is possibly true of all the zoosporic types, although certainly not the rule among the Oedogoniales for instance. Moreover, the zoospores which give rise to epiphytic *Oedogonium*, *Ulothrix*, *Cladophora*, etc. themselves in part arise from zygotes buried in the mud and thus the presence of such forms may depend primarily on suitable conditions for their germination obtaining in the mud and secondarily on the presence of a suitable substratum.

Most of the larger filamentous forms and many palmelloid types (e.g. *Tetraspora*) are, however, at the best only attached in the younger stages. With oncoming fragmentation they give rise to the familiar free-floating tangles, themselves colonised by epiphytes and inhabited by a special population of unicellular and colonial algae and animals, thus constituting secondary floating communities. These forms may thus belong to two communities, at first to the attached epiphytic and then to the floating community. It is possible that the floating communities of these forms will differ in some

respects according as they arise from primarily epiphytic stages or from stages which have been buried in the mud. In the latter case one would expect to find within them certain of the specific unicellular mud types, some of which may find favourable conditions for multiplication within the tangles.

In order to arrive at a clear understanding of the littoral algal vegetation, it is therefore necessary to know (a) the conditions affecting the germination of perennating stages in the bottom mud, and (b) the conditions determining colonisation of the primary substrata. The former can probably only be settled by experiment and scarcely any data are at present available, while the latter can at least in part be established by direct observation. A considerable number of observations of the latter type are in existence, but in most cases they do not go beyond the establishment of facts and the causal relations are mostly obscure. But it is these that require to be elucidated, if we are to arrive at the distinction of definite algal communities.

Important advances in the direction of distinguishing the attached communities are due to Willer (164, 165), Magdeburg (68), Oberdorfer (100), Karsinkin (53), Hurter (49), and Thomasson (142). There appears to be little doubt that a considerable number of Algae are practically indifferent to the nature of their substratum and the distribution of such forms depends probably in the main on the decreasing intensity of the light at progressive depths, as well as upon competition, although other factors will come into play. Willer (165, p. 39), however, points out that in general epiphytic growth shows a greater quantitative development on dead than on living substrata, and there is also often a qualitative difference (cf. also 38). As an instance he mentions that in the Müggelsee the stones were covered with an almost pure growth of *Epithemia zebra*, whilst the submerged plants bore no appreciable numbers of this diatom. According to the same authority *Cladophora* is found on stones, wood, and similar dead substrata, whilst submerged plants bear at the best but a very feeble growth of the species of this genus. The non-permanent character of the substratum, usually afforded by submerged macrophytes, is of course also a factor of importance.

Further data, furnished by Willer, refer to the effect of the nature of the living substratum. The growth on the shoots is quite different to that on the roots of *Lemna minor* and there are also appreciable differences between the upper and lower sides of the fronds, as well as between the basal and apical portions of the roots. Karsinkin (53) likewise found pronounced differences between the growth on the leaf-sheaths and on the internodes of *Equisetum limosum* (cf. also 14, p. 308). According to Willer *Cocconeis placentula* and *Protoderma viride* show a different distribution on the leaves of *Elodea* (cf. also 164, p. 64). When parts of the leaves die off, the *Cocconeis* collects especially on those that remain alive. The epiphytes in question tend to settle down in the grooves between adjacent epidermal cells resulting from the turgid condition of the latter (164, p. 62); it is suggested that, when parts of



the leaves die, the smoothing out of these grooves renders the substratum unsuitable for the attachment of the *Cocconeis* (165, p. 46). In some cases, moreover, the epiphytes show relations to one another. Willer (p. 51) mentions that stalkless species of *Gomphonema* often settle down on a zone of mucilage that surrounds the basal cells of epiphytic species of *Oedogonium* and that *Synedra ulna* favours the discs of *Protoderma*, without however being confined to them.

Analogous data are provided by Magdeburg (68, p. 137 *et seq.*) in relation to ponds. For a certain piece of water he states that *Coleochaete scutata* was mainly to be found on the under sides of *Potamogeton* leaves and on the stems of *Equisetum*, *Gongrosira debaryana* primarily on old parts of aquatics, *Protoderma viride* on stones and occasionally on dying parts of aquatics, *Aphanochaete repens* mainly on Algae and especially on *Oedogonium*, while young stages of *Oedogonium* and *Stigeoclonium* settled down anywhere where there was room. The examples<sup>1</sup> cited suffice to indicate an effect of the substratum which is, however, in many cases probably physical rather than chemical (14, p. 308). It will in the future be profitable to direct enquiry to the physical characteristics of the substratum and to distinguish categories of epiphytes according to their capacity to settle down on different types of surfaces (cf. 49, p. 203). In this connection it will be well to call to mind that forms like *Cladophora*, *Vaucheria*, *Oedogonium* are readily colonised by many epiphytes, their degree of suitability being apparently in the order named (cf. 49, p. 201), while the mucilaginous threads of the Zygnemales are usually practically immune, although here too there are differences of degree, since threads of *Mougeotia* more commonly bear epiphytes than those of other genera. Where epiphytes are confined to definite substrata, their periodicity is necessarily largely determined by that of the latter (31, p. 41; 47, p. 224) and there can be no doubt that in many cases the periodicity of the filamentous forms is influenced more or less markedly by the availability of the requisite substrata for the establishment of the primary epiphytic stages (32, p. 63; 68, p. 139). It must be emphasised, however, that a rational consideration of the algal communities, apart from the accompanying fauna, is not possible. As Willer mentions (164, p. 55; 165, p. 52), many of the animals, large and small, of the littoral zone feed on the epiphytic algal growth and the probability of some selection cannot be overlooked.

Brehm and Ruttner (14, p. 308) have also laid emphasis on the effect of the metabolism of the living substratum on the epiphytic growth inhabiting submerged plants. They indicate as specially important the local changes in oxygen content and in hydrogen-ion concentration. In the immediate vicinity of assimilating water plants the latter may change very appreciably to the alkaline side (pH 11), to become more neutral again after dark (pH 7.5). So

<sup>1</sup> Willer (164, p. 60) draws attention to the fact that, by contrast with those of the plankton, the epiphytic Diatoms have short squat frustules and have far fewer fat bodies.



marked a change towards the alkaline side results not only from the conversion of bicarbonates to carbonates, but also from a withdrawal of  $\text{CO}_2$  from the latter with the production of the hydroxide (cf. 69, p. 442; 114, p. 107). Hurter (49, pp. 203, 206) lays stress on the probable influence of nutritive substances diffusing from out of the substratum, and in this connection points out that, in the case of filamentous Algae, it is usually dead or dying parts that are colonised by epiphytes. At the present time, however, we are quite ignorant as to the possible effect of all these factors which are likely to play a more marked rôle in small stagnant waters than in larger ones. There is a wide field for enquiry here.

Apart from the effect of substratum, it is the diminution in light intensity as we pass to deeper and deeper layers of the water that most profoundly affects the nature of the epiphytic growth. It is, however, not always easy to separate this from other factors, such as the degree of movement of the water, the temperature relations, and the amount of available oxygen. As regards temporary epiphytes, the light factor merely limits the amount of substratum in the vertical direction, but in the case of the permanent epiphytes it undoubtedly conditions a zonation which is more or less marked. With reference to the former point, it may be noted that where the macrophytic growth is solely of the submerged type, the substratum which it affords may be too feebly illuminated to admit of the development of certain forms and that this may in some cases be the chief cause for their absence.

Oberdorfer (100) has recently dealt in great detail with the distribution of littoral Algae in the Lake of Constance in relation to the light factor (cf. also 49, p. 155 *et seq.*). The paper is distinguished by a specially careful analysis at different times of the year of the illumination at different depths and on substrata at various angles of inclination. The only forms that are recognised as euryphotic and apparently thriving equally well from the shore-line to a depth of 30 metres are Diatoms (species of *Cymatopleura*, *Amphora ovalis*, *Nitzschia communis*, *N. palea*, *Pinnularia major*, and perhaps also *Cymbella cuspidata*). The Algae of the shallower water (Fig. 4) are divided into two groups: (a) those which for the most part do not extend to a greater depth than 5 metres, the majority of these exhibiting a maximum growth in depths between a  $\frac{1}{2}$  and 2 metres (e.g. *Cladophora crispata*, *Oedogonium capillare*, *Draparnaldia plumosa*, *Navicula vuglare*); (b) those which are not usually found at a greater depth than about 15 metres (a few to 20 metres), while their maximum growth is between 2 and 10 metres depth (*Batrachospermum moniliforme*, *Epithemia argus*, *E. sorex*, *Mougeotia parvula*, *Tabellaria flocculosa*). Magdeburg (68, pp. 137, 157) gives similar data for pools of the Black Forest, while a number of observations indicate the effect of light in determining the growth of epiphytic forms on different substrata or on special parts of their substratum. Thus Willer (165, p. 41) mentions for a certain piece of water that *Fontinalis* with closely crowded leaves bore only blue-

green forms, while *Callitriche stagnalis*, affording much better conditions of illumination, was colonised solely by green forms (cf. also 57). Magdeburg (68, p. 137) describes how *Bulbochaete rectangularis* was to be found only on the upper sides of *Potamogeton* leaves, although the species of *Oedogonium* present settled down on both sides.

The various observations mentioned and many others indicate that there is a definite zonation in relation to increasing depth of water, but this zonation in the shallower water is usually rather obscure because few species are confined only to a limited depth, the majority occurring over a considerable range,

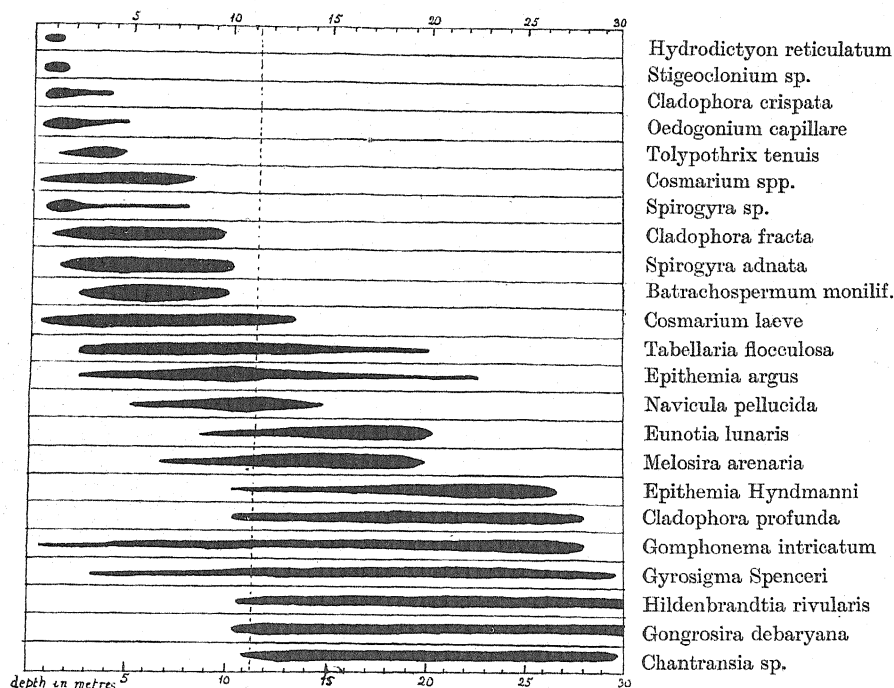


FIG. 4. Ranges in depth of typical species of freshwater Algae in the Lake of Constance (after Oberdorfer).

although usually developing a maximum growth only within a much smaller range. There is therefore a gradual change in the picture presented by the epiphytic growth as one passes into progressively deeper water, some forms fading out and others coming to the front, and it is only at greater depths, where the number of forms that can exist becomes much restricted, that the zonation really becomes sharply marked, so that definite communities are distinguishable (cf. below). Again local shading of the banks may lead to certain groupings appearing much nearer to the surface than they do in fully illuminated situations. It may be questioned therefore whether in the shallower water the light-factor can be used to demarcate communities, although

it conditions a zonation within many of those which consist of attached (epiphytic or bottom) forms. It seems probable, however, that the actual communities must be separated largely on the basis of substratum along the lines above indicated.

It is, moreover, certainly necessary to be on one's guard in ascribing all zonation merely to light effects. This is shown by Djakonoff's observations on the so-called periphyton on the Volga steamers (25). The three zones recognisable (*Pleurocapsa fluviatilis* above, then green Algae, and finally a stratum of Diatoms) are distinguishable not only in the vertical direction, but also from front to back; moreover the density of the strata produced by the various forms increases towards the stern of the steamers, no doubt in relation to the decreasing strength of the current.

Nor can there be much doubt that the well-marked belts of *Spirogyra adnata*, *Ulothrix zonata*, *Tolypothrix penicillata*, *Schizothrix*, etc. that have been recognised in various continental lakes (14, pp. 301, 330; 49, p. 119; 122, p. 40), wherever the shore is rocky, are largely conditioned in their extent by fall and rise of water-level, accompanied by wave action and consequent aeration (14, p. 310). The forms in question belong largely to those which Schröter and Kirchner (122, pp. 21, 43), in their classical work on the vegetation of the Lake of Constance, list as characteristic of the spray zone and which are supposed to depend for their existence on wetting by spray. Hurter (49, p. 118) has, however, pointed out that occasional spray is not sufficient for the development of these forms and regards these growths as representing submerged zones exposed by a recent fall of water-level. With him (*loc. cit.* p. 105) we can distinguish along the margin of every piece of water a permanently exposed zone, a permanently submerged zone, and a zone of oscillating water-level in which the prominent belts under discussion are for the most part found. Rise of water-level leads to the establishment of new growth within this zone, fall of water-level involves its gradual destruction as a result of desiccation, whilst a period of constant water-level is accompanied by gradual change in the growth as a result of the settling down of new forms and of the periodical succession. When the water-level rises certain forms (especially blue-green Algae) exhibit regeneration, which will ensue the more rapidly the shorter the period of exposure has been, but there is also colonisation by swimmers from the permanently submerged zone, and interesting data on the rapidity of such colonisation are given by Hurter (49, pp. 102, 110, 113). He also points out, however, that rapid rise of water-level may be accompanied by the formation of a persistent layer of air bubbles over the newly submerged surface which interferes with colonisation.

Brehm and Ruttner (14, p. 301; cf. also p. 339) mention that on the rocky south shore of the Untersee at Lunz the uppermost zone inundated only at high water is devoid of Algae, but bears a few lichens and mosses. Below this (Fig. 5) comes the *Tolypothrix penicillata* zone, which is recorded also from the lakes of Constance and Lucerne and appears to be widely represented in

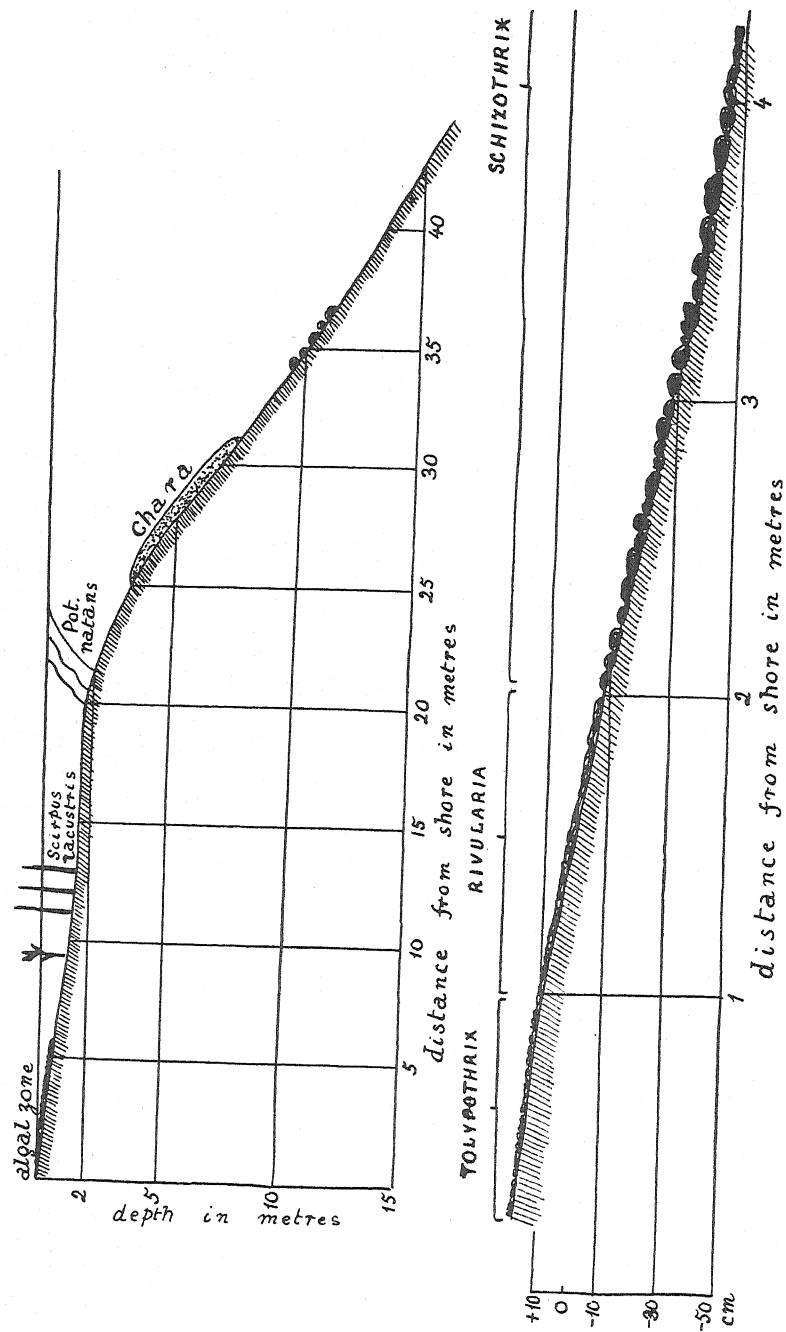


FIG. 5. Zonation of Algae in the Untersee at Lunz (after Brehm and Ruttner).

the uppermost part of the zone of oscillating water-level in many of the Central European lakes. It is often associated with *Scytonema myochrous*, which, according to Hurter, is an invader from the permanently exposed zone, and is sometimes overgrown by *Chroococcus varius*. Following on the *Tolypothrix* belt is one in which species of *Rivularia* (*R. Biasoletiana*, *R. haematites*) are dominant and this zone extends down into the permanently submerged region. The *Rivularia* is frequently associated with *Calothrix parietina*, as well as *Dichothrix gypsophila* and species of *Chaetophora*. Further down, within the permanently submerged zone, there is often a very extensive region occupied by the nodular and often calcified growths of species of *Schizothrix* (*S. fasciculata*, *S. lacustris*, *S. pulvinata*<sup>1</sup>), which, as it is not subject to desiccation or appreciable wave action, is far richer in associated Algae and animal life than the two preceding zones; *Ophrydium versatile* also has its chief centre here. Both Hurter (49, pp. 128, 136) and Zimmermann (172, p. 32) record dense growths of *Spirogyra* (*S. adnata* in the Lake of Constance) as extending to considerable depths (to 10 metres) on rocky shores. In both the Swiss lakes previously mentioned *Ulothrix zonata* forms occasional belts near the surface, but according to Oberdorfer (100, p. 503) it only occurs in quantity where there is an influx of organic matter.

The zonation just discussed, especially that occupying the region of oscillating water-level, is no doubt largely a result of the differing capacity of the diverse species to withstand desiccation, in which respect *Tolypothrix penicillata* appears to be the most resistant. It is, however, only where there is a firm rigid substratum that such zoning is recognisable. When the littoral region is sandy (30, p. 182) or muddy, as when the shore slopes more gently, the substratum bears a community composed largely of diatoms and blue-green Algae whose character changes as we pass into the deeper water and, after the belt of littoral macrophytic growth is left behind, becomes the very characteristic profundal community. This includes a rather limited number of species and has been studied in various continental waters (cf. 14, p. 319 *et seq.*; 22; 49, p. 137 *et seq.*; 50; 55; 100, p. 534 *et seq.*; 169, etc.), though, as far as I am aware, at present quite uninvestigated in British waters. Hurter (49, p. 243) mentions that occasional islands of rock, etc., projecting from the mud bear a markedly different growth, different too from that found on similar substrata in the littoral zone. It is not possible to deal here with the detailed composition of these mud communities, but a word may be added on the special conditions under which they exist.

The light intensity that is available for the photosynthesis of members of the profundal community<sup>2</sup> is of a very low order and all such forms must

<sup>1</sup> The *Schizothrix*-zone does not appear to be developed in this form in the Lake of Constance where, however, one finds the "Furchensteine" described by Schröter and Kirchner (122, p. 43; cf. also 100, p. 540) in which species of *Schizothrix* play a part.

<sup>2</sup> As regards the light factor in its relation to the development of phytoplankton in the deeper strata of the water, see 62.



possess a very low compensation point (i.e. the point at which photosynthesis and respiration compensate one another, so that the gaseous exchange is zero); in other words a large amount of the available energy must be used for photosynthesis and respiration must be at a minimum. In view of the frequent marked oxygen deficiency in the profundal region, a low respiration rate is probably in any case an essential for successful existence. In relation to the former point, Harder (45) has shown that shade plants of *Fontinalis* and *Cladophora* possess a much lower compensation point than sun plants (cf. also 115), which is ascribed to a reduced rate of respiration (100, p. 526). Oberdorfer further refers to work of Warburg and Naegelin (151) on the photosynthesis of *Chlorella* when exposed to minimal light intensities (0.1 per cent. sunlight) of such a value that the light was completely absorbed. As much as 73 per cent. of the available energy was found to be utilised and this is brought into relation to increased chlorophyll content (3.96 to 4.08 per cent. as compared with 1.8 to 2.6 per cent. in plants exposed to higher light intensities). In this connection it is significant that all the Algae of the profundal zone are deeply pigmented. Both Oberdorfer (100, p. 527) and Geitler (38, p. 98) comment on the reddish brown tint of the chromatophores of deep water Diatoms.

Diverse workers (37, 38, 172) have, moreover, described special deep-water communities composed very largely of red-coloured forms and exhibiting a very scanty representation of the green element. They have been recorded for the lakes of Constance and Lunz, but are not mentioned by Hurter in the lake of Lucerne, while Pascher (103) cites other instances from unnamed lakes in the Alps and in Holstein. Both Geitler (38) and Zimmermann list the same three creeping Algae (*Gongrosira debaryana*, *Bodanella Lauterborni* Zimm., a newly described fresh-water member of Phaeophyceae, and *Chantransia chalybea* var. *profunda*) as members of this community, which also comprises Diatoms and blue-green Algae. The red forms present are in part Florideae (*Hildenbrandtia*), in part red-coloured members of other groups; as examples may be mentioned *Rhodomonas* (Cryptophyceae) and diverse red Myxophyceae (species of *Oncobyrsa*, *Merismopedia*, *Oscillatoria* and *Chamaesiphon incrustans*). A curious feature of these communities is that only some forms assume the red colour, quite a number of normally coloured blue-green forms being, for instance, always present.

Zimmermann in the lake of Constance distinguishes two communities found at different depths, viz. (a) the *Cladophora profunda*-*Chamaesiphon incrustans* (red) community, including a violet-coloured *Oscillatoria* (*O. Lachneri*), and (b) the *Hildenbrandtia rivularis*-*Bodanella Lauterborni* community, in which the above-mentioned *Chantransia* is most commonly found. The former community is abundant between 10 and 20 metres depth, while below that it is confined to better-illuminated spurs, while the latter is found between 15 and 35 metres, but in the upper part of its region of occurrence is mainly found in shaded furrows of the rock. According to Zimmermann



transitions between the two are far rarer than the pure communities. In the lake at Lunz the rock is covered by ooze from a depth of 15 metres onwards and so the two communities are not recognisable there. In this lake, however, the deep-water forms are also to be found on the meadows of *Fontinalis*, although there are naturally certain differences resulting from the different nature of the substratum; amid the foliage of the moss one finds *Rhodomonas* and deep blue species of *Cryptomonas*.

There can be little doubt that the minimal development of green forms and the prevalence of other, and especially of red, colorations represents a definite adaptation on the part of these deep-water communities to the quality of the light that reaches them. It would be remarkable if similar communities were not to be found in British waters.

The occurrence of abundant loose-lying, often more or less spherical masses (the epiphythemic formation of Naumann), on the bottom in the littoral zone and sometimes well out into the deeper water is a phenomenon that has long been known for the aegagropilous *Cladophoras* (cf. e.g. 13) and certain other forms. Recently, however, Naumann (88, who gives the earlier literature) and Decksbach (23) have appreciably added to our knowledge of such forms which, apart from the *Cladophoras* and *Ophrydium versatile*, all belong to the Myxophyceae (species of *Chroococcus*, *Aphanocapsa*, *Aphanothece*, *Nostoc*, *Rivularia*, and aegagropilous species of *Tolypothrix* and *Scytonema*). They appear to be more distinctive of eutrophic than of oligotrophic waters, but are in no way restricted to the former. Naumann points out that, while the aegagropilous types show a more or less marked periodical occurrence, the others are to be found all the year round, which suggests that the former are but a special phase of development of species that for the rest belong to other (probably bottom) communities. This, however, is likely to be true of all of them and the conditions that bring about their remarkable development in some waters and not in others still remain to be investigated. According to Naumann the communities under discussion are characterised by their purity and usually consist of but a single species, but Gams (35) states that this is by no means always the case.

The aegagropilous Myxophyceae play a great rôle in precipitating lime. In this connection it may be recalled that Murray (75, p. 74) has described the formation of spherical calcareous pebbles on the bottom of Lough Belvedere near Mullingar in Ireland by *Schizothrix fasciculata*, while according to Rothpletz (113, p. 265) oolitic calcareous grains are produced by species of *Gloeocapsa* and *Gloeothece* on the shores of the Great Salt Lake, Utah. According to Naumann, moreover, all the loose-lying forms precipitate some iron, especially in older stages; this is especially striking in the case of *Nostoc Zetterstedtii*, where even small fragments of iron ore may be produced. There can be no doubt that such loose-lying communities play a rôle in the gradual accumulation of sediment.

The foregoing matter will have shown that a basis for the rational distinction of algal communities is gradually being reached, although much still remains to be done. There can be little doubt that the direction of further progress lies in the study of micro-communities (68, p. 131). Of the plankton, since that is receiving abundant attention I will not speak, save to emphasise once again that what is most needed at the present time is the elucidation of its origin and its relation both to the littoral and the bottom communities. More difficult of investigation are the floating tangles of filamentous Algae found in the littoral zone and such a prominent feature of most shallower waters; they would best be spoken of as floating macro-communities. I believe that the most fruitful line of attack will be to take them individually, and it will be simplest in the first place to commence with such as are dominated by a single filamentous form and to determine its usual associates. This must, however, go hand in hand with a study of the micro-environment, i.e. of gas content, pH, and other determinable features within such tangles during day and night and at different seasons during their period of occurrence. Investigation of the epiphytic communities, as far as they inhabit living substrata, will have to follow the same lines, but in this case a study of surface in relation to the distribution of epiphytes is also necessary. Another aspect of the problem lies in the relation between the epiphytic and the floating macro-communities, as well as between the bottom communities and the latter. And all this detailed analysis will have to be fitted into the general scheme of classification of waters into oligotrophic, eutrophic, etc.

On the preceding basis we may undertake a primary broad classification of the algal communities of static waters as follows:

A. *Attached communities*, among which we shall have to distinguish the forms which are permanently and those which are only temporarily attached, the latter subsequently belonging either to the plankton or to the floating macro-communities. Here belong:

(a) *Epiphytic communities*, varying with the nature of the substratum, the light intensity, etc.

(1) On inorganic substrata (stones, rocks, etc.).

(2) On organic substrata which may be (a) living, or (b) dead.

(b) *Silt (bottom) communities* which will vary with the depth and the degree of opacity of the water, as well as with the nature of the sediments.

B. *Floating macro-communities*, among which we have to distinguish those arising from the bottom and those which are derived from primarily epiphytic stages. They will themselves bear some epiphytic growth and include a considerable number of littoral planktonic forms.

C. *Loose-lying communities* (p. 264).

D. *Plankton* (littoral and pelagic, p. 245).

In flowing waters only the attached communities and the plankton are present, the latter consisting of detached members of the former (and especially

of their reproductive bodies) and of material introduced from tributaries, backwaters, and other sources of supply. In the absence of floating macro-communities flowing waters afford a simpler problem, but the continuous movement of the water introduces a new factor which greatly increases the difficulties of detailed analysis.

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## SYMPOSIUM ON XEROMORPHY

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MAXIMOV, N. A. The physiological significance of the xeromorphic structure of plants.

HUBER, BRUNO. Die Trockenanpassungen in der Wipfelregion der Bäume und ihre Bedeutung für das Xerophytenproblem. (2 Figs.)

SCHRATZ, EDUARD. Zum Vergleich der Transpiration xeromorpher und mesomorpher Pflanzen.

THODAY, D. The significance of reduction in the size of leaves.

### THE PHYSIOLOGICAL SIGNIFICANCE OF THE XEROMORPHIC STRUCTURE OF PLANTS

By N. A. MAXIMOV.

THE question of the peculiarities that characterise the xeromorphic structure and the physiological significance of these characters is one of the most important and interesting problems in plant ecology and at the same time it is being much disputed. Its solution may be approached from two points of view. Either only one side of the plant life may be taken into consideration, namely its water relations, as the most important under conditions of dry habitats. Or the whole life of desert plants is considered as a unique integral process, although built up of different and even antagonistic links, but having as the main result the accumulation of organic substance and the creation of conditions for reproduction. Authors, who try to explain anatomical and morphological peculiarities of desert plants considering only their water regime, very often accept a teleological point of view and advance the proposition that in dry environments the plants must make economical use of water and that therefore their whole structure must be directed toward a decreased transpiration. The supporters of this view, therefore, accuse a number of plants of being "false" xerophytes, since from their structure alone they cannot be included in this scheme (Kamerling, 1914). They seek a basis for their views mainly in the study of the anatomy of desert plants and describe with enthusiasm thick cuticle, wax cover, sunken stomata, covering hairs and a number of other characters which, according to their opinion, must lower the transpiration rate of the desert plants to a scarcely noticeable minimum. Those who take up this position have seldom used precise physiological experiments, apparently believing that anatomical data give sufficiently good indications of the nature of the water relations of these plants. And only in recent times do we find on their part any attempts at an experimental confirmation of their views (Seybold, 1929).

Those who support the other, mainly physiological, point of view (Maximov, 1916, 1926; Huber, 1924; H. Walter, 1926; Stocker, 1928) do not refuse to study the structure of desert plants. But they do not attempt to reconstruct physiological processes from anatomical data alone. There are too many examples in the history of the science in which such purely speculative constructions have led to entirely wrong conclusions. The danger of interpretation of these speculations increases as they are accepted and quickly reproduced in popular literature. Later it requires much labour to destroy these rapidly rooted, false conceptions. In this respect, the problem reminds one in many ways of the fight waged round the subject of weed vegetation.

In other words, from my point of view, anatomical investigations must always be followed by physiological experiments in order to show the real correlation between structure and function.

The physiological peculiarities and the structure of xerophytes that inhabit desert and semi-desert habitats are extremely varied, depending upon the numerous possible means of adaptation to the very complex and varying conditions of the desert. Thus the use of the combined methods of anatomical and experimental study does not enable us to interpret all the most characteristic peculiarities of the xeromorphic structure. Different types of xerophytes possess such sharply differing structures and modes of life, that it appears nearly impossible to find characters common to all of them. More precise knowledge of xeromorphic structure and corresponding function can be obtained more conveniently by another method, namely the study of the direct action of desiccating factors upon the structure and the physiological functions of the plant organism. For this purpose, the plants are cultivated with different soil moisture contents or with different air moisture contents or with different light intensities; or the plants are subjected to a single wilting or to repeated wiltings, and to other modifications of the environment.

A series of investigations that will not be described in detail here, since they have been given in my recently published book, *The Plant in relation to Water*, have shown that under desiccating conditions we always get changes in one direction, namely, the decrease of the dimensions of all the cells, including the guard cells of the stomata, increase in the number of stomata per unit of area, a more compact network of veins in the leaf, denser hair covering, thicker cuticle and wax covering, and very often an increased development of the palisade tissue and a decreased development of the spongy tissue. Physiologically these changes are followed by an intensive ventilation of the leaves and create conditions favourable to increased assimilation and in many instances to increased transpiration.

The indications of a high transpiration rate in xerophytes, which I first published in 1916 on the basis of my investigations in Tiflis, and which were confirmed later in a series of papers by other authors (Alexandrov, 1922; Huber, 1924; Stocker, 1928; Walter, 1926, and others), seemed then, and still

seem to some, paradoxical and quite unacceptable. Some authors, as for instance Seybold in his paper "Die physikalische Komponente der Transpiration" (1929 a), disputes my results on the basis of experiments conducted to determine the transpiration of plants of different ecological types, and returns to the earlier statement of Schimper, that the characteristic peculiarity of xerophytes is the decreased transpiration. It is to be regretted that the experiments of Seybold, although carried out very accurately, cannot be considered as answering the question, since he never used a true xerophyte in his experiments; as examples of xerophytic plants he used mostly the leaves of evergreen trees. And after all, if it is necessary to create a group of "false xerophytes," the evergreens would be the right group of plants to which to apply the term. It is known from botanical geography that evergreen trees are quite definitely adapted to the more humid maritime climate (compare for instance the well-known scheme of Brockmann-Jerosch and Rübel) and the transition to the drier continental climate results in their disappearance and the substitution of deciduous trees. This picture is very striking in Transcaucasia. In the very humid western part of the range, where the precipitation reaches 2000 to 3000 mm. a year, the "xerophytes" studied by Seybold (*Hedera helix*, *Laurus nobilis*, *Taxus baccata*, *Ilex aquifolium*) growing in the dense shade of the deciduous forests, are very characteristic. These species all disappear entirely in the drier forests of the eastern part of Transcaucasia. And in the real desert of course none of the xerophytes that Seybold studied could survive.

Later Seybold (1929 b) undertook a special journey in the Egyptian-Arabian desert in order to become directly acquainted on the spot with the transpiration of real desert plants. Here by a number of experiments he became convinced that desert xerophytes, as for instance *Zygophyllum coccineum* and *Erodium glaucophyllum*, very often transpire water much more extensively than such a mesophyte as *Sonchus oleraceus*, which he used for comparison. And he thus became compelled to acknowledge that under certain circumstances ("unter Umständen") xerophytes transpire more than mesophytes. To save the theory of Schimper, Seybold introduces in this paper the conception of "transpiration resistance" (Transpirationswiderstand) and tries to show that this resistance is much higher in xerophytes than in mesophytes.

The method of determining transpiration used by Seybold was, however, not perfect. He determined the loss of water from detached branches, which he placed without water in direct desert sunlight and wind for fully 15 minutes. There is no doubt that he was dealing not with the transpiration of normal turgid plants, but with those which were more or less wilted. And as we shall see later the transpiration resistance increases very rapidly during wilting, and in different degrees and with different rapidities in mesophytes and in xerophytes. Furthermore these experiments of Seybold's do not give quite reliable material for the judgment of the real transpiration of desert plants.



The approximate determinations he made have shown that all the xerophytes he investigated possess a higher resistance than the mesophytes. This result was naturally to be expected, since he was dealing—as has already been mentioned—with plants in a state of fairly strong wilting and just under these conditions the anatomical peculiarities of xerophytes manifest their action in the clearest way. Thus we can draw no conclusions from the experiments of Seybold about the behaviour of xerophytes under conditions when their stomata are widely open and their leaves fully turgid. Therefore even in modified form the traditional conception of the decreased transpiration of xerophytes does not appear convincing.

My assistant, Vasiljev, who worked in 1929 in the Kara-Kum desert in Turkestan, undoubtedly one of the driest places in the world, was able to verify my observations on the high transpiration of xerophytes (Vasiljev, 1931). He used a very accurate and precise method of determining transpiration by weighing detached branches of plants on a torsion balance at very short intervals of time never exceeding a minute (Huber, 1927; Richter and Strachov, 1929), and came to the conclusion that such typical shrubs of this desert as *Ammodendron Conollyi*, *Smirnovia turkestanica* and others have a very high rate of transpiration. Another assistant of mine, Kusmin, who works in the desert near Baku and who has studied the transpiration of the well-known "camel thorn" (*Alhagi camelorum*) and of other xerophytes, obtained the same results (Kusmin, 1930).

I therefore feel the right to affirm that the high rate of transpiration of many xerophytes is a firmly established fact. By this I do not mean that all xerophytes without exception must possess a very high transpiration rate, because, as I have already mentioned, the xerophytes are a very diversified group, different representatives of which may possess quite different physiological characters. As an example, I may mention as typical of one type of such plants the cacti, which are so characteristic of the deserts of America, and of the other type, *Alhagi camelorum*, *Peganum* and *Zygophyllum* of the deserts of the Old World. In these two groups we find neither anatomical nor physiological peculiarities of similar character. Keeping in view this extremely great diversity in the structure of xerophytes and the impossibility of discovering characters that are common to all, one has thus either to refuse entirely the concept of xeromorphic structure or to base it chiefly on the changes in structure produced in the plant under the influence of the desiccating factors. The character of these changes has already been mentioned. What is their physiological significance?

One cannot understand this physiological significance by selecting from the whole cycle of life processes one particular function, as for example, transpiration, and then trying by every possible means to find an environmental adaptation which lowers it. It is necessary to take the life cycle of the desert or the semi-desert plant in its entire complexity, and to follow its peculiarities of structure as related to these life processes.

The necessity of approaching the problem of xeromorphism, not dogmatically but logically, is particularly prominent in this connexion. One must never forget that the main contradiction of the life of every fully grown plant, especially of a desert plant, the antagonism between the processes of photosynthesis and water balance, manifests a deep influence upon its structure. The same stomatal openings serve for the diffusion of carbon dioxide into the leaf and for the diffusion of water vapour out of the intercellular spaces into the surrounding atmosphere. Therefore plants cannot stop their water loss without decreasing their photosynthetic activity. For the retention of water they must pay with hunger in carbon and for their supply of carbon they have to pay with increased water loss. Such is the dilemma which confronts plants of dry habitats, and brings about an immense diversity of forms and types of xerophytes.

To evaluate the adaptation of plants to desert conditions, it is necessary to remember that the climatic conditions of deserts are characterised by extreme variation: in other words, very great amplitudes of fluctuation in temperature, as well as in humidity, occur both annually and daily. The desert, therefore, is not a uniformly and constantly heated oven, as is imagined by some botanists who have never been in deserts or have seen them only in passing. On the contrary, deserts are sometimes very cold and sometimes very humid. The very life of most desert plants depends upon their ability to profit from more or less short and comparatively favourable periods. And in desert localities where no such periods occur and where no precipitation falls for several years, as happens in the Djungara valley in Chinese Turkestan, no vegetation whatever develops, as has been shown by the recent expedition of Vavilov and Popov.

The active vegetative life of the majority of desert plants takes place chiefly in these short periods of comparatively favourable conditions—during rains, for example, and in the short period that immediately follows when water is available for plant growth. This activity occurs chiefly in the morning hours when the plants are sufficiently saturated with water that has accumulated in the tissues during the nocturnal stoppage of transpiration. The chief type of desert plant, and the most widely distributed, is the type of the ephemerals, which develop rapidly and are able to complete their life cycle during a comparatively short rainy period. During this period the ephemerals cover the soil of the desert with a uniform green carpet, which is the main source of food for the herds of the desert nomads. The physiology of the ephemerals has not yet been investigated. The rapidity of their development presupposes that they have a high assimilation rate, which is correlated with an energetic, rapid aeration of the leaves, and therefore with a high transpiration rate. I have recorded a very high intensity of transpiration rate in plants of the spring vegetation of the semi-desert habitat in the vicinity of Tiflis, plants which are closely related in physiological character to the desert ephemerals.

Plants of the more perennial type, which keep their leaves for a longer period, continue their assimilatory activity during the hot, dry period only when their root systems develop unusually deep and reach the ground waters. Among the plants of this type are the "camel thorn" (*Alhagi camelorum*), *Peganum*, and many of the woody plants of the sandy deserts. Experiments show that all these plants possess a very high rate of transpiration, and it is among them that we generally find those with the highest transpiration rate. The leaves of such plants, as investigation shows, usually possess a sharply defined xeromorphic structure—small cells, numerous stomata, a very dense network of conducting bundles, all characters which indicate that large amounts of water are carried through them. The high transpiration rate results in a direct advantage—the evaporation of large quantities of water lowers the temperature of the leaves and in this way prevents protoplasmic changes and injury from high temperatures in the desert environment. And yet at the same time these plants are such typical desert plants that it is not reasonable to deprive them of the name of xerophytes. The most varied and complicated group of plants among the so-called xerophytes are those whose root systems do not reach the ground waters, and yet are not ephemerals, but keep their living parts during the entire year or at least during the frostless period of the year. These plants must live on reserves of water obtained from the comparatively shallow layers of the soil; on reserves that are replenished very scantily and occasionally during the dry period of the year and often not at all until the next rainy season.

It is among plants of this type that one would look for the so-called typical xerophytes, which, according to Schimper and his followers, must be distinguished by an economical expenditure of water. And in reality, we find them here. First of this group are the cacti and other succulents, which store large reserves of water in the tissues of their stems and leaves during rainy periods, and then slowly expend it during many months. It is of interest that not only the water, but also the carbon utilisation of these plants is based to a great extent upon the use of their own reserves. In the dry period of the year their stomata, which are not numerous, are tightly closed. The carbohydrates that are produced from the carbon dioxide formed in the process of respiration during the night and from the organic acids under the catalytic activity of the light, serve as a source for the carbon nutriment of these plants. Such an unusual physiological function results in the absence of any xeromorphic structure, except a very thick cuticle. Structurally, these plants remind one of the hydrophytes with very large cells and few stomata. From the physiological point of view as well as from the anatomical, and also from their very peculiar appearance, they present a quite separate group that has nothing in common with other desert plants.

On the other hand, among the desert plants with restricted water supply we also find a group that is marked by a very high rate of transpiration.

According to our experimental data the desert species of *Artemisia*, *Centaurea*, *Parthenium* and others can be listed in this group. At first sight it seems quite incomprehensible that these plants, having at their disposal so little water, should spend it so extravagantly, and yet at the same time remain undoubtedly well adapted to their existence under dry conditions. In order to clear up such a contradiction, it is necessary to recall that the rate of transpiration is a varying factor, which depends to a large degree upon a series of external as well as internal conditions which vary with different plants and especially with plants of distinctly different ecological groups.

The absence of parallelism in these groups is due to two main causes: in the first place the correlation between the cuticular and the stomatal transpiration. The determinations of Kamp show that the cuticular transpiration of mesophytes is but 2 to 5 times lower than the stomatal, while with leaves having a thicker cuticle it is in some cases as much as 25 times lower. It is clear therefore that with plants of the second type the transpiration will decrease much more when the stomata close, than with plants of the first type, and therefore all the factors influencing the opening or closing of the stomata will affect plants of the second type more than those of the first. The second cause is the difference in sensibility to external influences of the stomatal apparatus in various plants. As a series of experiments show, under a deficiency of water the stomata of mesophytes close sooner than those of xerophytes, and the former will therefore lower their transpiration rate sooner than the latter.

Let us imagine for example two plants, one of a xeromorphic structure, the other of a mesomorphic character, which under conditions of sufficiently high moisture and in a moist atmosphere have identical rates of transpiration. Now let us follow their changes in transpiration rate under conditions of increasing desiccation. The mesophytic plant, at the beginning of the change, will have a markedly increased transpiration rate, but very soon the absorption of water will not replace the loss from transpiration and the deficit will cause the stomata to close. The transpiration at this stage will decrease considerably and assimilation will stop entirely. But because of the high cuticular transpiration the loss of water will continue at a rapid rate, the plant will wilt, and in continued drought will dry out entirely.

The behaviour of the xeromorphic plant under the same conditions will be quite different. The transpiration rate will again increase at first, and as the stomata remain open for a longer time under the combination of external factors, this plant will lose more water through the stomata than a mesophyte. As I have shown long ago in co-operation with my co-workers, this is not a great danger, as its tissues can endure a considerable dehydration without injury; in other words, this plant is drought resistant. The assimilation will also continue much longer in this plant than in the mesophyte. This is without doubt an important advantage the xerophyte possesses over the mesophyte.

Sooner or later, however, the stomata in the xeromorphic plant will also close, and only the cuticular transpiration will take place. As the cuticle of the xerophyte is much less permeable, especially when somewhat dry, the quantity of water lost will be decreased very quickly to a minimum and the plant, although in the state of permanent wilting, will remain alive for a long time with only small quantities of water lost from the tissues. Later, when a more humid period again occurs, the xerophytic plant will recover and start its vegetative activity anew.

The physiological relationship of the two plants will correspond when we consider the experimentally determined transpiration rates—the higher rate of transpiration will occur in the xerophytic plant. With the increased transpiration there is also an increased rate of assimilation in the xerophyte. But when the state of wilting is reached, the water economy of the xerophyte will be much greater. Here then is a distinctly different physiological behaviour of the plants when supplied with plenty of water and when in a state of wilting. To my mind, here is the key to the explanation of the seeming contradiction between the high transpiration rate and the necessity for protection against drought in xerophytic plants. *It is not the rate of transpiration when an abundant water supply is present, but the capacity to restrict water loss to a minimum in time of drought, that characterises the water utilisation of the xerophyte.* Nor is this in disagreement with our understanding of the xeromorphic structure of the plant. Increased aeration of the leaves, with open stomata, more rapid assimilation under these conditions, and reduction of water loss through the cuticle, which guarantees maintenance of the necessary minimum water content—these features, in my opinion, make up the physiological significance of the xeromorphic structure.

Likewise from this point of view, the function of the different adaptations for the protection of the leaf surface, for example the waxy covering, the abundant development of cuticle, the hairs, and other anatomical peculiarities, becomes more clearly defined. In the conception of the early authors these structures functioned directly in reducing the rate of transpiration of xerophytes and yet our experiments show that they are inefficient in this respect. It is not difficult to understand the inefficiency of anatomical structures such as the thick cuticle or the wax cover in protecting the plant from excessive transpiration when the stomata are open, just as the best heat insulation of the walls of a house will not keep it warm in winter when all the windows are opened wide. But when the plant is wilting, when its stomata are closed and when the loss of water takes place only through the cuticle, then all these anatomical peculiarities which are so numerous and which are described so readily by anatomists and morphologists, manifest their protecting properties. The explanation of the physiological basis of xeromorphism and the significance of xeromorphic structure from the physiological point of view, which I advance, does not in the least deny the signifi-



cance of these adaptations in the water economy of the plant, as is sometimes thought. It simply assigns to them another significance and, as it seems to me, one which is more in accord with the experimentally established facts.

From the same point of view I am inclined to appraise the conception of "transpiration resistance," introduced by Seybold (1929 *b*). This expression was taken by Seybold from the science of electroconductivity and he tries to apply to the loss of water by the plant the law of Ohm, taking the transpiration resistance as inversely proportional to the transpiration intensity and directly proportional to the deficit of humidity (saturation deficit) on the surface of the transpiring system of the plant.

Thus the "transpiration resistance" of Seybold is to a certain extent the obverse of the "relative transpiration" of Livingston. The very uncertain determination of the "transpiring power" of the atmosphere by means of different kinds of atmometers and evaporimeters, which give results not comparable with one another, he replaces by determination of the saturation deficit on the plant surface, and this is a step in the right direction. But this step forward is at the present time rather imaginary, because for a precise determination of the saturation deficit it is quite necessary to know the real temperature of the transpiring surface—a problem that is not yet solved in a satisfactory form in spite of a number of more or less successful attempts. Seybold himself confesses that he did not succeed in measuring satisfactorily the transpiration resistance of the desert plants which he studied.

In the recent, mainly German, literature my views are considered as a complete antithesis of Schimper's. Schimper declared that xerophytes are characterised by a decreased transpiration. The authors referred to say that Maximov contradicts Schimper and declares that xerophytes are distinguished by an increased transpiration rate. Such a formulation seems to me to be a pure misunderstanding. I have never desired nor tried to contradict Schimper and have always had a feeling of the greatest respect for his attempt—almost heroic for the time—to bring physiological principles into the study of phytogeographical problems. Very naturally this heroic attempt could not be quite free from mistakes, and among them I reckon the theory of the transpiration criterion as a deciding factor in the determination of xerophytes. This is said with no desire to depreciate the great merits of Schimper, but a fundamental study of the problem under the conditions at the Tiflis laboratory has convinced me that the transpiration criterion as advanced by Schimper is incorrect and incomplete, and that another term, which is full of significance as applied to xerophytes, namely *drought resistance*, must be substituted. The rate of transpiration by itself does not tell us anything about the proper classification of a plant as a xerophytic or a mesophytic type; the xerophytes are not distinguished by decreased transpiration, but by the capacity to survive long periods of drought and dehydration of their tissues without injury, or with only slight injury. This thesis I have advanced many times,



and I consider it to be now more firmly established than ever by experimental evidence. How, it may be asked, did Schimper's transpiration criterion for xerophytes originate, how could such a careful observer, a man who travelled so much, and saw with his own eyes all the types of the vegetation—how could he make such a mistake? The explanation is that the mistake is by no means complete. There is undoubtedly an element of truth in Schimper's theory, because all xerophytes have a decreased *cuticular* transpiration. When, in the critical period of drought, the plant is in danger of drying out the stomata are closed, and a very economical use is made of the last remaining water.

If we are to return to Schimper, as some German authors believe we should, then we must not attempt to bring to life again the transpiration criterion which is now only of historical interest, but we must correct his definition of xerophytism. In a corrected form it will read as follows: Xerophytes are plants of dry habitats which are able to decrease the transpiration rate to a minimum when under conditions of water deficiency. But such a definition, with which I fully agree, is after all not a return to Schimper, but an advance from Schimper, an advance made without throwing aside anything of value in his definition, and at the same time avoiding a mistaken theory which may have been quite inevitable 30 years ago, but which we cannot any longer maintain.

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# DIE TROCKENANPASSUNGEN IN DER WIPFELREGION DER BÄUME UND IHRE BEDEUTUNG FÜR DAS XEROPHYTENPROBLEM<sup>1</sup>

VON BRUNO HUBER.

(Mit 2 Abbildungen im Text.)

ICH benütze gerne die Gelegenheit, über den Fortgang jener Untersuchungen zu berichten, die mich in den Jahren 1922–1924 zur Ablehnung des Transpirationskriteriums der Xerophilie führten, zu derselben Zeit als in Mittel- und Westeuropa die grossartigen Untersuchungen Maximows (19, 20) bekannt wurden, die—von ganz anderem Beobachtungsmaterial ausgehend—zu ähnlichen Folgerungen geführt hatten.

Ich darf zunächst in kurzen Zügen die Ausgangsbeobachtungen in Erinnerung bringen. Ich hatte mich mit der Transpiration der Bäume in verschiedener Stammhöhe beschäftigt und gefragt, ob der zunehmenden Erschwerung der Wasserversorgung ein sparsamerer Wasserverbrauch, also eine Abnahme der Transpiration entspreche. Es war ein glücklicher Zufall, dass ich meine Untersuchungen an einem 15 Meter hohen Exemplar einer *Sequoia gigantea* begann, dem höchsten Baum, der mir damals im Garten der Hochschule für Bodenkultur in Wien zur Verfügung stand (9). An diesem Baum ist nämlich bei rascher Wägung abgeschnittener Zweige<sup>2</sup> tatsächlich fast immer ein sehr ausgeprägter Transpirationsabfall in der Krone festzustellen, wie dies für einen bestimmten Fall die Kurve 1 der Abb. 1 zeigt: die Transpiration in 12 Meter Höhe beträgt hier nur noch etwa die Hälfte, in anderen Fällen sogar nur ein Viertel bis ein Sechstel der in 2 Meter Höhe gemessenen<sup>3</sup>. Dabei beruht der Abfall nicht etwa auf einem verschiedenen Bau der Zweige, sondern stellt zweifellos nur eine Reaktion auf die erschwerte Wasserversorgung dar; denn die Unterschiede verschwinden nach längeren Regenperioden oder wenn man die abgeschnittenen Zweige in Wasser stellt.

Als ich meine Untersuchungen auf weitere erreichbare Bäume ausdehnen wollte (10), stiess ich auf unerwartete Abweichungen. An einer 12 m hohen *Quercus pedunculata* war von einem Transpirationsabfall nichts zu bemerken: im Gegenteil, wenn ich mit Kobaltpapier und Alkohol-Tropffläschchen auf meinen Versuchsbaum stieg, konnte ich in der Wipfelregion fast stets eine

<sup>1</sup> Vortrag, gehalten im Symposium über "Xeromorphie" auf dem V. Internationalen Botanischen Kongress in Cambridge, 19. August 1930.

<sup>2</sup> Ueber die Methodik der Transpirationsbestimmung vergl. Huber (13), Iwanoff (15) und Stocker (23).

<sup>3</sup> In 14 Meter Höhe folgt noch einmal ein leichter Anstieg der Transpiration, der auf korrelativer Förderung des Wipfels beruht.

grössere flächenrelative Transpiration und weiter geöffnete Stomata feststellen<sup>1</sup>. Bei rascher Wägung abgeschnittener Zweige ergab sich folgendes Bild:

	2 m.	6 m.	12 m.
Transpiration in mg. pro 100 cm. <sup>2</sup> und Stunde	46	49	76
Oberflächenentwicklung in cm. <sup>2</sup> pro Gramm Frischgewicht	150	127	89
Transpiration in mg. pro Gramm Frischgewicht und Stunde	69	65	67

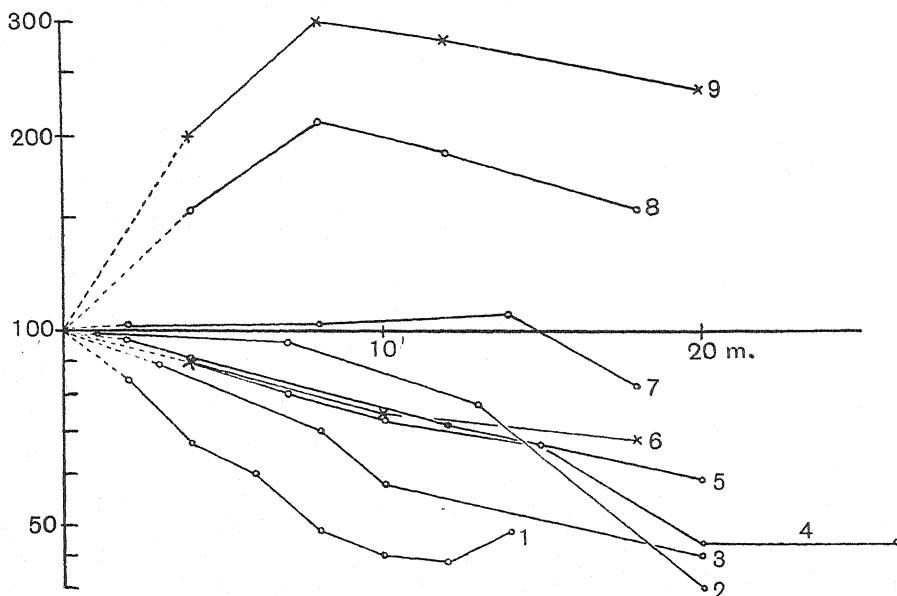


ABB. 1. Transpiration in verschiedener Stammhöhe. Abszisse—Stammhöhe in Metern; Ordinate—Transpiration, bezogen auf den (linear extrapolierten) Null-Meter-Wert (Teilung logarithmisch). 1. *Sequoia gigantea*; 2. *Fagus sylvatica*; 3. *Tilia grandifolia*; 4. *Picea excelsa*; 5. *Acer pseudoplatanus*; 6. *Quercus sessiliflora*; 7. *Fraxinus excelsior*; 8. *Larix leptolepis*; 9. *Pinus austriaca*.

Wenn wir die Transpiration auf gleiches Frischgewicht der Blätter beziehen, sind die Unterschiede gering; i.a. finden wir einen leichten Anstieg nach oben. Die geringere Oberflächenentwicklung der Wipfelblätter wird durch eine bedeutend grössere Transpiration der Flächeneinheit kompensiert.

Zwischen meiner *Sequoia* und der Eiche bestand nun ein auffälliger Unterschied: bei *Sequoia* waren keine wesentlichen Veränderungen im Bau der Zweige aus den verschiedenen Höhen zu bemerken; die Blätter der Eiche

<sup>1</sup> Völlig übereinstimmende Befunde hat Stålfelt in sehr ausgedehnten Untersuchungen an der Fichte erzielt (22, s. u.), wobei er auf die Uebereinstimmung mit meinen Angaben ausdrücklich hinweist. Auch Gradmann und Guttenberg geben ähnliche Unterschiede im Spaltöffnungsverhalten von Sonnen- und Schattenblättern mediterraner Gehölze an. Es mutet daher etwas eigentümlich an, wenn neuestens Kerl (17) in Unkenntnis der übrigen Literatur meine Befunde anzweifelt, weil er an einer 4 m hohen Buchenhecke (!) und einer ca. 9 m hohen *Quercus pedunculata* solche Unterschiede nicht finden konnte.

zeigten dagegen in grösserer Höhe in ausgeprägtestem Masse den *Uebergang zu den bekannten xeromorphen Merkmalen der sogenannten Sonnenblätter*: sie waren kleiner, dicker, stärker gelappt, die Oberfläche etwas wellig und unregelmässiger zum Licht orientiert wie die der "Schattenblätter" aus tieferen Kronenteilen. Wir stehen also vor der Tatsache, dass mit dem Auftreten der Sonnenblättrigkeit ein Ausbleiben—oder sagen wir richtiger, ein Hinausschieben—der zu erwartenden Transpirationseinschränkung parallel geht.

Dieser Antagonismus zwischen morphologischer Trockenanpassung und Transpirationsabfall in der Krone liess sich auch quantitativ erhärten, sobald ich wesentlich höhere, 20–30 m hohe Bäume in den Kreis der Untersuchung zog (11). Die Abb. 1 führt Ihnen die wesentlichsten Ergebnisse vor, die im altehrwürdigen Gehölzbestand des Forstversuchsgartens Mariabrunn bei Wien gewonnen wurden, der Stätte, wo Höhnel seine klassischen Transpirationsbestimmungen der Forstgehölze ausgeführt hat. Wir können hier in 16 bis 26 m. Höhe bei allen geprüften Bäumen eine Transpirationseinschränkung gegenüber der Kronenbasis feststellen, aber sie ist von recht verschiedenem Ausmass. Am deutlichsten ist sie bei den sogenannten "Schattenhölzern" *Fagus*, *Tilia grandifolia* und *Picea excelsa*, wenn auch in keinem Fall so stark wie bei *Sequoia*; schwächer ist sie bei *Acer pseudoplatanus*, *Quercus sessiliflora*, am schwächsten bei *Fraxinus*, *Larix* und schliesslich *Pinus austriaca*. Im grossen und ganzen können wir sagen, dass gerade die Gehölze, die als empfindlich gegen Trockenheit gelten wie *Fagus*, *Picea*, und *Tilia* auf die Erschwerung der Wasserversorgung mit der Stammhöhe durch eine viel stärkere Transpirationseinschränkung reagieren wie die widerstandsfähigeren Arten *Quercus* und *Pinus*. Wir vermuten, dass die schon äusserlich sichtbaren xeromorphen Merkmale der letzt genannten Arten wohl vereint mit nicht ohne weiteres erkennbaren inneren Eigentümlichkeiten die Ursache sind, dass die plumpste aller Anpassungsmöglichkeiten an erschwerte Wasserversorgung, die Einschränkung des Wasserverbrauchs sparsamer angewendet werden kann. Damit hat aber die Transpirationseinschränkung, die so lange als das ausschlaggebende Merkmal der Xerophyten, ja geradezu als Masstab der "Xerophilie" galt, ihre Bedeutung eingebüsst und ist zu einem Kriterium zweiten oder dritten Ranges herabgesunken, das überdies nur mit grosser Vorsicht angewendet werden darf!

Bevor wir diese Gedanken weiter ausführen, müssen wir unsere Tatsachenkenntnis noch nach einer Richtung erweitern: 20 Meter Höhenunterschied am Baum bedeuten noch immer keine allzugrossen Unterschiede in der Wassersättigung; auch die untersten Zweige und Blätter sind meist noch ein Stück von voller Sättigung entfernt, die obersten in der Regel noch immer turgeszent. Wie verhalten sich nun Zweige aus verschiedener Stammhöhe bei anderen als den natürlichen Wassergehalten? Solche Bestimmungen liegen von meiner Versuchseiche vor. Wenn abgeschnittene Sonnen- und Schattenzweige 24 Stunden in einer feuchten Kammer gehalten wurden, wobei die Schnittflächen in Wasser tauchten, so zeigte sich nachher die Transpiration

der Schattenzweige ganz bedeutend, oft auf mehr als das Doppelte, die der Sonnenzweige dagegen nur unwesentlich erhöht. Das beweist neuerdings, dass die mehr mesomorphen Schattenzweige schon auf das am Baum bestehende Sättigungsdefizit mit einer viel schärferen Transpirationseinschränkung antworten als die Sonnenzweige<sup>1</sup>. Es lehrt aber ausserdem, dass *unter optimalen Wasserverhältnissen* die Schattenblätter—und wie wir vorgreifend verallgemeinern, die Mesophyten—zweifelloos stärker transpirieren als die Sonnen-

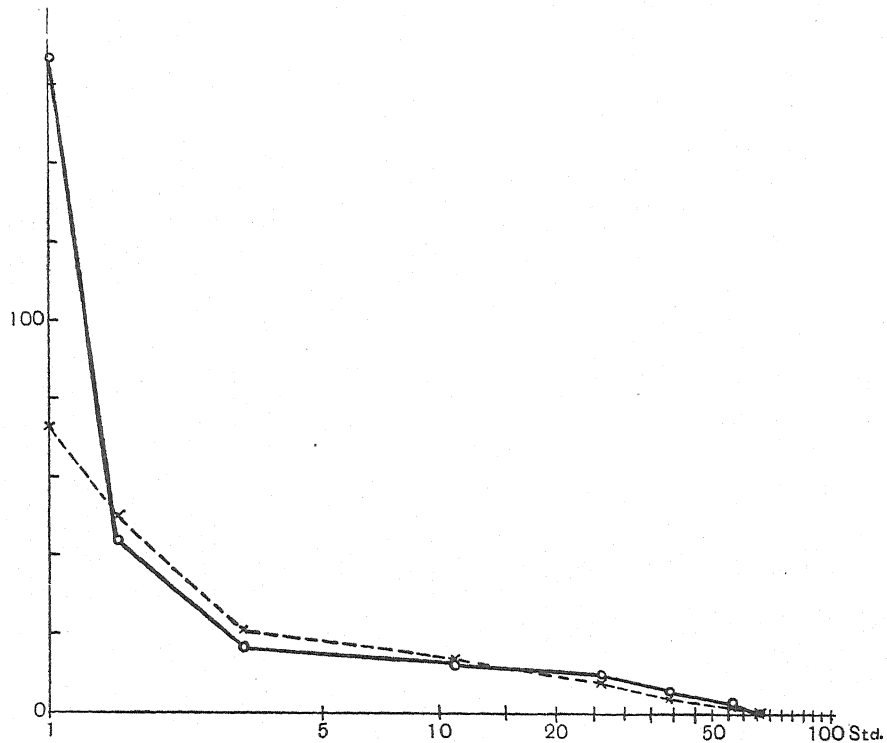


ABB. 2. Transpirationsrückgang abgeschnittener Schattenzweige aus 2 m (ausgezogene Kurve) und Sonnenzweige aus 12 m Stammhöhe (unterbrochene Kurve) einer *Quercus pedunculata*. Abszisse—Zeit in Stunden (logarithmische Teilung); Ordinate—Transpiration in Milligramm pro Gramm Frischgewicht und Stunde.

blätter bzw. Xerophyten. Wenn sie es unter natürlichen Bedingungen oft nicht tun, so beruht das auf der hohen Empfindlichkeit der Mesophyten schon gegen geringe Wasserdefizite. Bei Bäumen bieten Stamm- und Stockausschläge oft gute Gelegenheit, sich von der hohen Transpiration gut mit Wasser versorgter Schattenblätter zu überzeugen.

Als gegenteiliges Experiment kann man nun Schatten- und Sonnenzweige trocken liegen lassen und den Transpirationsabfall bei sinkendem Wassergehalt verfolgen. Dabei bietet sich das oben stehende Bild (Abb. 2). Schon in der ersten

<sup>1</sup> Auch die Transpiration der Sequoiazweige steigt auf ein Mehrfaches an, wenn man sie abschneidet und in Wasser stellt.

Stunde fällt die Transpiration der Schattenzweige unter die der Sonnenzweige und bleibt zunächst kleiner, sodass nach 15 Stunden die Wasserverluste 44 und 58 Prozent des Anfangsgehaltes betragen. Dann aber kehrt sich das Verhältnis um und die Sonnenzweige transpirieren deutlich (mitunter mehr als die Hälfte) weniger als die Schattenzweige und zwar auch noch, wenn ihr Wassergehalt wieder höher liegt als der der Schattenzweige. Offenbar kommt eben erst jetzt nach völligem Spaltenschluss ihr besserer Kutikularschutz zur Geltung. Der Erfolg ist, dass die Sonnenzweige erst zwei Tage später lufttrocken werden, was natürlich zu einem nochmaligen Ueberschneiden der Transpirationskurven führt. In unserer Abbildung ist das nicht mehr dargestellt, weil es sich dabei schon nur noch um stündliche Transpirationswerte unter 1 mg. pro Gramm Frischgewicht handelt.

Wir können zusammenfassend die Eigentümlichkeiten der Schattenblätter der unteren Kronenteile und der Sonnenblätter der Wipfelregion durch folgende Sätze kennzeichnen:

(1) Mit der Ausbildung xeromorpher Strukturen ("Sonnenblättrigkeit") geht eine Verzögerung der sonst bei erschwerter Wasserzufuhr beobachteten Transpirationseinschränkung parallel. Je ausgeprägter xerophil die Bäume nach Morphologie und Standortsansprüchen sind, desto schwächer ist der Transpirationsabfall mit der Stammhöhe.

(2) Bei extremer Erschwerung der Wasserversorgung im Experiment (Liegenlassen abgeschnittener Zweige) erweist sich die *Fähigkeit zu Transpirationseinschränkung* bei den xeromorphen Sonnenblättern den mesomorphen Schattenblättern überlegen. Ebenso ist bei voller Wassersättigung die Transpiration der Schattenblätter eindeutig höher.

In welcher Beziehung stehen nun diese Feststellungen zum Xerophytenproblem? Ich behaupte: *die Anpassungen, die wir in der Wipfelregion der Bäume gegenüber tieferen Kronenteilen feststellen können, sind auch für eine ganze Gruppe von Xerophyten gegenüber Meso- und Hygrophyten typisch.*

Den Beweis wollen wir in drei Schritten führen: Dass der Vergleich *in bezug auf den Standort* zulässig ist, scheint mir sicher. Wir sprechen von einem trockenen Standort, wenn die Wasseraufnahme erschwert oder die Gefahr der Wasserabgabe erhöht ist. Beides trifft für die Wipfelregion der Bäume zu: die Wasserleitung durch den hohen Stamm bedeutet eine Erschwerung der Wasseraufnahme, deren Grösse wir dank den Saugkraftmessungen und Untersuchungen des Wasserleitungssystems der letzten Jahre annähernd quantitativ angeben können. Dass die Verdunstung in der Wipfelregion gesteigert ist, bezeugen die Atmometermessungen des Amerikaners Gates (4) und des Verfassers (12).

Dieser Vergleichbarkeit der Bedingungen entspricht eine weitgehende Gleichsinnigkeit der Anpassungseinrichtungen. Für die *morphologischen Anpassungsmerkmale* kann diese Uebereinstimmung schon lange als bewiesen gelten: alle Züge der äusseren Morphologie wie des feineren anatomischen



Baues, die für die Sonnen- gegenüber den Schattensprossen charakteristisch sind, kehren bei Xerophyten wieder. Ich brauche nur daran zu erinnern, wie getreu die quantitativ anatomischen Merkmale die Zalski für Blätter verschiedener Insertionshöhe festgestellt hat (s. Maximow (21), S. 328ff.), in Kellers Untersuchungen verwandter Arten trockener und feuchter Standorte wiederkehren. Auch das Bild, das Maximow von typischer Xeromorphie entworfen hat (vergl. den vorangehenden Aufsatz), die Abnahme der Zellgrösse, die steigende Zahl der Stomata, das dichtere Gefässbündelnetz und die Verstärkung der Kutikula, passt Zug für Zug auch auf die Sonnenblätter.

Den Untersuchungen der letzten Jahre aber blieb es vorbehalten, zu zeigen, wie weitgehend auch die *Uebereinstimmung im physiologischen Verhalten* ist. Vor allem hier wie dort die überraschende Feststellung, dass die Transpirationseinschränkung unter Bedingungen ausbleibt, wo wir sie bei Mesophyten und Schattenblättern längst hätten erwarten müssen. Hand in Hand damit geht die Erkenntnis, dass es beim Kampf ums Wasser entscheidendere Hilfsmittel gibt als die Transpirationseinschränkung. Ich möchte aber mit grösstem Nachdruck betonen, dass diese Feststellung einer oft verhältnismässig ansehnlichen Xerophytentranspiration *nur ein Teilergebnis aus einem verwickelteren Komplex* ist. Weil es für weite Kreise das überraschendste Ergebnis der Xerophytenforschung der letzten Zeit war, ist es geradezu unter dem Schlagwort einer "lebhaften Xerophytentranspiration" zu einseitig in den Vordergrund geschoben und zu voreilig verallgemeinert worden. Es war mir daher eine besondere Freude, aus den vorstehenden Ausführungen Maximows entnehmen zu können, dass wir uns über folgende Einschränkungen vollkommen einig sind: erstens ist unter optimalen Bedingungen die Transpiration der Mesophyten vielfach überlegen und nähert sich der Xerophytentranspiration nur bei gelinder Erschwerung der Wasserversorgung, wie das wohl Iljin (14) zum erstenmal gesehen und betont hat; vor allem aber scheinen unter wirklich extremen Bedingungen die Xerophyten wohl fast stets zu einer besonders wirksamen den Mesophyten überlegenen Transpirationseinschränkung befähigt, zu der sie nur viel seltener greifen müssen als die Mesophyten. Die Transpiration ist eben bei den Xerophyten ganz einseitig zugunsten der jederzeit kontrollierbaren stomatären Transpiration verschoben, wie ich schon 1924 nachdrücklich betont habe.

Ich kann zu diesen Fragen einige neueste Angaben aus unveröffentlichten Untersuchungen meiner Schülerin Frl. H. Heilig machen<sup>1</sup>. Diese hat im Kaiserstuhl, einem Xerophytengebiet der oberrheinischen Tiefebene vier charakteristische Standorte regelmässig kontrolliert. In einem xerophilen Kiefernwaldchen stieg zu unserer Ueberraschung die Bodensaugkraft selbst während des trockenen Sommers 1928 nicht über  $3\frac{1}{2}$  atm. Diese Trockenheit genügte, um die empfindlicheren Pflanzen des Standorts zu Transpirationseinschränkung und Spaltenschluss zu zwingen, während sie den Xerophyten des

<sup>1</sup> Die Arbeit ist inzwischen in *Zeitschr. f. Botanik*, 24 (1931), 225 erschienen.

Standorts begreiflicherweise nichts anhaben konnte. So fanden wir mehrmals *Fagus* und *Convallaria* schwach, *Viburnum lantana*, *Quercus sessiliflora*, *Bupleurum falcatum* und vor allem *Geranium sanguineum* viel stärker transpirierend. Anders liegen die Verhältnisse auf dem extremen waldfreien Südhang des "Badberg." Hier übersteigen die Bodensaugkräfte auch in der Wurzelregion mehrfach 100 atm. und die meisten Pflanzen gehen während des Sommers ein. Die wenigen überdauernden Xerophyten zeigen dann ausgeprägte Transpirationseinschränkung; man kann sie besonders leicht feststellen, wenn man mit Exemplaren derselben Arten vergleicht, die wenige Meter tiefer auf dem feuchteren Talboden stehen. Auch am Badberg findet man aber in den frühen Morgenstunden die Stomata häufig geöffnet, und die widerstandsfähigsten Arten wie *Teucrium montanum* sind dann die letzten, welche sie zwischen 7 und 8 Uhr schliessen.

Das Ergebnis eines vertiefteren Einblicks ist also, dass die Frage der Xerophytentranspiration überhaupt nicht mit einem einzigen Schlagwort zu beantworten ist; das wesentliche ist ein verschiedenes physiologisches Verhalten der Xerophyten und Mesophyten bei einsetzender und fortschreitender Trockenheit. Das Verhältnis zwischen Xerophyten- und Mesophytentranspiration ist daher nicht konstant, sondern je nach den Bedingungen einem dauernden Wechsel unterworfen, wobei offenbar in einem ziemlich grossen Bereich die Xerophytentranspiration überlegen sein kann. Das Problem lässt sich heute nicht mehr auf die einfache Schimpersche Fragestellung zurückschrauben! Mit diesen Feststellungen glaube ich mich nicht nur in Uebereinstimmung mit den vorstehenden Ausführungen Maximows, sondern auch mit den wichtigen experimentellen Untersuchungen von Iljin, Boysen-Jensen, Alexandrov und Frl. Dietrich zu befinden.

Bezüglich einiger weitere Punkte muss ich mich auf kurze Andeutungen beschränken. Ich kann es aber nicht unterlassen, auf die subtilen Spaltöffnungsuntersuchungen Stälfelts u. a. hinzuweisen. Diese liefern in schönster Weise das notwendige Gegenstück zu den Transpirationsmessungen; sie haben auch den Parallelismus zwischen Sonnenblättern und Xerophyten weiter bestätigt. Immer wieder hat sich gezeigt, dass die Stomata der Mesophyten und Schattenblätter viel empfindlicher reagieren, die der Sonnenblätter und Xerophyten viel nachhaltiger und gleichmässiger geöffnet sind. Nicht nur in Russland, auch im Mediterrangebiet, in Aegypten, in Ungarn sind Xerophyten während der Trockenzeit mit geöffneten Spalten angetroffen worden, und wenn wir Frl. Henrici glauben dürfen, gehen viele Steppengräser des Bechuana-landes eher zu grunde als dass sie ihre Stomata schliessen.

Der Raum verbietet es, auch noch auf die osmotischen Verhältnisse der Sonnenblätter und Xerophyten vergleichend einzugehen. Nur auf eines möchte ich hinweisen: Frau Krasnosselsky-Maximow hat zuerst erkannt, dass Xerophyten durch grössere Dehnbarkeit ihrer Zellwände an stärkere Wassergehaltsschwankungen ohne Turgeszenzverlust angepasst sind, und verschiedene

neueste Untersuchungen haben diese Angabe gerade für Sonnenpflanzen in ausgedehntem Masse bestätigt (vergl. Heilig und die dort angeführte Literatur). Auch xerophile Standortmodifikationen derselben Spezies sind durch erhöhte Membranelastizität ausgezeichnet. Solche Formen sind daher auch für Saugkraftbestimmungen nach den Methoden von Ursprung und Blum (24) vielfach besser geeignet als Schattenpflanzen und Hygrophyten.

Ich bin am Schlusse meiner Ausführungen und glaube sagen zu dürfen: Es gibt einen zweifellos weitverbreiteten Xerophytentyp, der in der Art seiner Einstellung auf Trockenheit mit den Sonnenblättern aus der Wipfelregion der Bäume übereinstimmt. Ich möchte vorschlagen, diese Anpassungsform als "*Sonnenpflanzentyp*" zu bezeichnen, und damit zugleich die Ueberzeugung zum Ausdruck bringen, dass es sicher auch noch andere Typen der Trockenanpassung gibt. Der abweichende Typus der Sukkulenten ist ja schon lange erkannt und in seiner Sonderstellung ausreichend gekennzeichnet. Um die Abgrenzung weiterer, wohl weniger tiefgreifend unterschiedener ökologischer Gruppen ist augenblicklich die Standortforschung sichtlich bemüht. Sie wird auch für die Verfeinerung unserer Vorstellungen vom Sonnenpflanzentyp von Bedeutung sein.

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# ZUM VERGLEICH DER TRANSPIRATION XEROMORPHER UND MESOMORPHER PFLANZEN<sup>1</sup>

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Bei dem Studium der Transpirationsintensität verschiedener Pflanzengruppen haben von jeher diejenigen Arten, die xeromorph ausgebildet, und daher nach Schimper mit Mitteln zur Einschränkung der Transpiration ausgestattet sind, in besonderem Masse interessiert. Nach zahlreichen Untersuchungen am Standorte kamen jedoch eine Reihe von Forschern zu der Ansicht, dass die Transpiration der xeromorphen Pflanzen keineswegs geringer sei als die der mesomorphen. Hiergegen wurden in jüngster Zeit wiederum Zweifel erhoben von solchen Autoren, die die xeromorphe Struktur vom physikalischen Standpunkte aus als Verdunstungswiderstand aufgefasst wissen wollen, eine Ansicht, die vor allem von Seybold vertreten wird.

Zu dieser Frage sollen hier einige Gesichtspunkte geäußert werden, zu denen in dem extremen Trockengebiet von Süd-Arizona angestellte Untersuchungen berechtigen.

Zunächst mögen einige Worte darüber gesagt werden, ob die bei ökologischen Untersuchungen bisher allgemein benutzte Methode, den Verlust abgeschnittener Pflanzen während einer längeren Zeitperiode festzustellen, geeignet ist, etwas über die absolute Transpirationsgrösse auszusagen. Die Beobachtung des Verdunstungsvorganges von abgeschnittenen Pflanzen in kurzen Zeitabschnitten, wie 1 oder 2 Minuten, lässt deutlich erkennen, dass es nicht berechtigt ist, zum mindesten unter extremen klimatischen Bedingungen, den Wasserverlust während einer längeren Zeit als konstant anzusehen. Es ist sicher, dass der Wasserverlust in den einzelnen Zeitabschnitten kein gleichmässiger ist, sondern in den meisten Fällen mit fortschreitender Zeit abnimmt. Die Abnahme der Verdunstungswerte ist vor allen von drei Factoren abhängig. Zunächst ist von Bedeutung, wie hoch die tatsächliche Transpiration zur Zeit des Abschneidens der Pflanze ist, sodann spielen eine grosse Rolle die zur Zeit der Wägung herrschenden Aussenbedingungen. Ausserdem ist der Abfall der Verdunstungsgrösse abhängig von der Struktur der Pflanze.

Das Zusammenwirken dieser Factorenkomplexe kann zu den verschiedensten Resultaten führen. Als allgemein gültig lässt sich feststellen, dass die Verdunstungswerte desto stärker abfallen, je mesomorpher eine Pflanze ist,

<sup>1</sup> Nach einer Mitteilung, gegeben auf dem V. Internationalen Botanischen Kongress in Cambridge. Die ausführliche Arbeit ist erschienen in *Jahrb. für wiss. Bot.* 74, 1931.

je höher die absolute Transpiration zur Zeit des Abschneidens war, je länger die Zeit nach dem Abschneiden bis zum Zurückwägen beträgt und je grösser das Dampfdruckdefizit der Luft während der Untersuchung ist.

Kurzfristige Wägungen lassen somit zu dem Schlusse kommen, dass Verlustwerte, die aus längeren Zeiträumen (10 bis 60 Minuten) gewonnen sind, durchaus kein Mass für die absolute Transpiration sind, ja dass unter extrem trockenen und heissen Bedingungen selbst Wägungen im Abstände von einer Minute noch keine Auskunft über die normale Transpirationshöhe geben können. Derartige Methoden lassen nur relative Verdunstungswerte gewinnen, wenn die zu vergleichenden Pflanzen gleichzeitig oder gleich nacheinander untersucht werden. Eine solche vergleichende Untersuchung ist desto eher möglich, weil der Abfall der Verdunstungswerte zu irgend einer Zeit in einer bestimmten Beziehung zu dem Anfangswerte, und somit wohl auch zu der normalen Transpiration steht.

Bestehen nun bestimmte Unterschiede zwischen der Transpirationsgrösse xeromorpher und mesomorpher Pflanzen? Es ist zunächst nötig, sich darüber klar zu sein, von welchem Standpunkte aus diese Frage beantwortet werden soll. Man kann sie vom ökologischen Gesichtspunkte aus studieren, das heisst, feststellen, wie verhalten sich die verschiedenen Pflanzenarten am Standorte unter den natürlicherweise herrschenden Bedingungen, oder aber man kann die Verdunstung der Pflanze vom rein physikalischen Standpunkte aus auffassen, indem man die Pflanze als spezielles Verdunstungssystem ansieht. Wie wir sehen werden, dürfen aber Befunde der einen Forschungsrichtung nicht ohne weiteres auf die andere übertragen werden.

Vom physikalischen Standpunkte aus hat Seybold diese Frage angegriffen und ist zu der Überzeugung gekommen, dass xeromorphe Pflanzen unbedingt einen grösseren Verdunstungswiderstand besitzen müssen. Es dürfte auch wohl keinem Zweifel unterliegen, dass diese Ansicht richtig ist. Wenn wir zwei Verdunstungssysteme haben, die sich *nur* in ihrer Struktur unterscheiden, sich aber sonst in allen die Verdunstung beeinflussenden Factoren gleich sind, und auch unter gleichen Aussenbedingungen stehen, so ist es sicher, dass das am stärksten xeromorphe System die geringste Verdunstung aufweisen wird.

Als allgemeine Folgerung aus solchen Untersuchungen kann aber nur abgeleitet werden, dass mit stärkerer xeromorphen Ausbildung ein höherer Widerstand ausgeübt wird. Der weitere Schluss, dass deshalb xeromorphe Pflanzen auch eine geringere Gesamttranspiration haben müssen als mesomorphe, ist jedoch nicht mehr zulässig. Denn während der Verdunstungswiderstand tatsächlich in erster Linie von der Struktur abhängt, wird die endgültige Höhe der Transpiration noch von einer Menge weiterer Factoren bedingt.

Streng genommen lässt sich aus der Blattstruktur und dem von ihr geleisteten Widerstand nur dann ein Schluss auf die absolute Transpirationshöhe ziehen, wenn es sich um ein und dieselbe Pflanze in verschiedener Ausbildung



hinsichtlich ihrer Struktur handelt. Sobald aber mehrere verschiedene Arten vorliegen, deren Verdunstungswiderstand auf Grund ihrer Strukturen in einem bestimmten Verhältnis zueinander stehen, braucht sich dieses nicht in der Menge des abgegebenen Wassers zu äussern. Es ist also nicht angängig, auf Grund morphologischer Messungen über die Blattstruktur die Transpirationsgrösse einer Pflanze voraussagen zu wollen, was durchaus möglich wäre, wenn nur die Struktur diese Grösse bestimmen würde. Da wir aber bei jeder Pflanzenart ausser den strukturellen Verschiedenheiten auch spezifische physiologische Eigenschaften voraussetzen müssen, lassen sich Befunde an einer Art nicht auf eine andere übertragen.

Es ist daher auch nicht möglich, auf Grund solcher Untersuchungen, in denen die Beziehungen zwischen Struktur und Verdunstungswiderstand an ausgewählten Pflanzentypen gemessen wurden, die tatsächliche Transpirationsgrösse der Pflanzen am Standorte beurteilen zu wollen, oder allgemein festzustellen, dass xeromorph ausgebildete Arten am Standorte weniger transpirieren als mesomorphe.

Am Standorte haben wir es mit vollkommen anderen Verhältnissen zu tun. Während wir bei der Untersuchung der Verdunstungswiderstände im Laboratoriumsexperiment unter sonst gleichen Bedingungen arbeiten können, kommen bei der Untersuchung im Freien eine Reihe von Factoren unbekannter und unbestimmbarer Grösse hinzu, die ihrerseits auf die Wasserabgabe einen grossen Einfluss ausüben können. Bei dem Studium der Transpiration im Freien können wir daher lediglich Beobachtungen über die tatsächliche Wasserabgabe anstellen, ohne aber daraus Schlüsse auf die spezielle Wirkung der Struktur machen zu können, da ja zu viele unbekannte Factoren mit im Spiele sind. Ganz gleichgültig wie die Resultate derartiger Bestimmungen sein mögen, zu einem Kriterium der physikalischen Ergebnisse über den Verdunstungswiderstand können sie nicht ausgewertet werden, ebensowenig wie das Umgekehrte möglich ist. Die tatsächliche Transpirationshöhe am natürlichen Standorte ist ganz unabhängig von dem Resultate der physikalischen Analyse. Trotz hohen Widerstandes mag doch die Gesamttranspiration sehr hoch sein.

Zunächst kann sich die Struktur eines Blattes, d.h. Dicke der Kutikula, Wachüberzug, Behaarung u. ä. wesentlich nur auf die kutikuläre Transpiration auswirken. Die Höhe der Transpiration wird aber in viel grösserem Masse von der stomatären Transpiration bedingt. Letztere hat ihrerseits nur wenig mit dem Vorhandensein xeromorpher Merkmale zu tun. Eine gleichzeitige Reduzierung von Zahl und Grösse der Stomata mit xeromorpher Struktur ist als allgemeine Regel noch nicht nachgewiesen. Es ist somit durchaus möglich, dass eine Pflanzenart einen durch ausgesprochene Xeromorphie bedingten Widerstand durch grössere und zahlreichere Stomata wieder ausgleicht.

Ausser der Struktur des Blattes sind nun eine Reihe von anderen Factoren für die tatsächliche Wasserabgabe verantwortlich, die bei jeder Pflanzenart und zu jeder Zeit sich verschieden auswirken. Es ist zu beachten, dass wir am

natürlichen Standorte niemals Pflanzen unter gleichen Bedingungen haben können. Im besten Falle können wir gleiche klimatische Bedingungen erwarten. Aber darüber hinaus schafft sich jede Pflanze selbst spezifische Unterschiede, die bei der Beurteilung der Transpiration berücksichtigt werden müssen.

Eine besonders wichtige Rolle bei der Wasserabgabe spielt z.B. das Wurzelsystem und die damit zusammenhängende Wasserversorgung. Es ist eine recht allgemeine Erscheinung, dass einer oberirdischen xeromorphen Struktur eine besonders starke Entwicklung des Wurzelsystems entspricht. Schon aus diesem Grunde kann eine Pflanze mit hohem Verdunstungswiderstande unter Umständen eine bedeutend höhere Wasserabgabe leisten als eine mesomorphe Art mit nur oberflächlichen Wurzeln. Bei mesomorphen Arten werden wir daher viel öfter mit beschränkter Wasseraufnahme als "limiting factor" rechnen müssen.

Daher ist es von vornherein nicht zu erwarten, dass sich zwischen der in der Natur zu beobachtenden Transpirationshöhe und der Blattstruktur bestimmte Korrelationen aufstellen lassen. Untersuchen wir die Pflanzen eines Standortes oft genug, d.h. unter den verschiedensten Verhältnissen, denen sie normalerweise ausgesetzt sind, so sehen wir bald, dass sich die einzelnen Arten bezüglich ihrer Transpirationshöhe nicht in fester Reihenfolge anordnen lassen, sondern dass diese sich von Fall zu Fall ändert. Während wir unter bestimmten Bedingungen finden mögen, dass eine Art doppelt soviel transpiriert als eine zweite, kann unter anderen Bedingungen das Verhältnis umgekehrt sein. Die einzelnen Arten werden von einer Änderung in den Aussenbedingungen in ganz verschiedener Weise beeinflusst. Daher ist es nicht gängig, aus dem Befunde zu einer willkürlichen Zeit nun allgemeine Schlussfolgerungen ziehen zu wollen, oder das einmal festgestellte Verhältnis nun als Norm anzusehen.

Wenn wir alle auf die Transpiration einwirkenden Factoren berücksichtigen, lassen sich die in der Natur beobachteten Verhältnisse gut verstehen. Auch wenn wir nicht im Stande sind, die Grössenordnung, in der einzelne Factoren wirken, genau festzulegen, so ist es immerhin möglich, und vorläufig ausreichend, zu wissen, in welcher Richtung sie sich auf die Transpiration auswirken.

Vergleichen wir bei den Untersuchungen im Freien die festgestellten Transpirationshöhen mit der Menge des Wassers, das den Pflanzen zu Verfügung stand, bedingt entweder durch den Wasservorrat im Boden oder auch durch die Ausbildung des Wurzelsystems, so lassen sich recht deutliche Beziehungen finden. Mesomorphe Arten übertreffen im Allgemeinen die Xeromorphen in ihrer Transpirationshöhe nur dann, wenn die Wasseraufnahme in keiner Weise gehemmt war. In einem Trockengebiet findet das nur recht selten statt, nämlich nur nach einem genügenden Regenfall. Sobald aber die Untersuchungen zu einer Zeit angestellt werden, wo die Wasseraufnahme beschränkt ist, wird man meistens finden, dass mesomorphe Arten in ihrer Transpiration hinter den Xeromorphen zurückbleiben. Denn diese leiden wegen ihres ober-

flächlichen Wurzelsystems am ehesten unter erschwelter Wasserversorgung, während die Xeromorphen auf Grund ihrer grosse Bodenmassen durchsetzenden Wurzeln noch für lange Zeit eine genügende Wassermenge aufnehmen können, um eine hohe Transpirationsrate aufrecht zu erhalten. Daher ist es gar nicht verwunderlich, dass Forscher, die ihre Untersuchungen in extremen Trockengebieten anstellten, zu der Überzeugung kamen, dass xeromorphe Pflanzen eine hohe Transpirationsrate besitzen, und diese Befunde bestehen auch sicherlich ganz zu Recht.

Nur muss dabei im Auge behalten werden, dass es sich lediglich um die Beantwortung der Frage handelt, wie gross die Transpirationshöhe unter "natürlichen," aber unbekannten Bedingungen ist. Im Grunde genommen handelt es sich bei solchen Untersuchungen nur um einen Vergleich von Standort zu Standort. Mögen die untersuchten Arten auch derselben Pflanzengesellschaft angehören, so hat jedes einzelne Individuum doch physiologisch seinen eigenen Standort, wenn wir z.B. an die Verschiedenheiten der unterirdischen Teile denken. Das Resultat solcher Untersuchungen darf daher nicht zu Schlüssen ausgewertet werden, dass die Pflanzen mit niedrigerer Verdunstung auch den höheren Widerstand ausgeübt hätten.

Zusammenfassend möchte ich sagen, dass feste Beziehungen zwischen der Struktur der Blätter und ihrer am Standorte zu beobachtenden Transpiration nicht bestehen. Die maximale Transpirationshöhe der xeromorphen Arten braucht nicht hinter der der mesomorphen Arten zurückzubleiben, da ein durch die Struktur bedingter Widerstand durch andere Factoren aufgehoben werden kann. Es darf wohl als gesichert gelten, dass die normale Transpiration xeromorpher Pflanzen eine recht hohe ist. Eine stärkere Transpirationstätigkeit der xeromorphen Pflanzen steht aber in keinerlei Widerspruch zu dem aus physikalischen Gründen zu fordernden grösseren Widerstand xeromorpher Strukturen.

## THE SIGNIFICANCE OF REDUCTION IN THE SIZE OF LEAVES

By D. THODAY.

REDUCTION in size of leaves is one of those features which have been regarded as adaptations for reducing transpiration. There is enough correlation between small-leaved plants and dry situations to have lent colour to the view.

But Warming (36, p. 111) long ago remarked that the shoots possessing pinoid, ericoid or cupressoid leaves "are usually extremely rich in leaves." It is surprising that this fact should not have attracted more attention, for it is obvious that a sufficiently large number will make up for small size.

It is not possible on mere inspection to say whether a shoot with many small leaves exposes less or more surface than a shoot with fewer large leaves. But for microphyllous species the estimation of leaf area is in itself a matter of difficulty. Often only a rough approximation is possible after considerable expenditure of labour.

Moreover, as soon as a comparison between contrasted types is suggested, the question obtrudes itself, what should be the basis of comparison? In relation to what quantity is reduction of surface advantageous?

A basis commonly used is unit fresh weight of leaves. Now the reciprocal of surface per unit weight is a rough measure of succulence. For this purpose unit weight of contained water might be a better basis (for example, in comparing hard-leaved with soft-leaved plants) though a less convenient one. Variations in water content introduce some uncertainty in either case. Shoot (or leaf) volume, even if it can be measured accurately, is an ambiguous basis, since the proportion occupied by air spaces varies so much.

If, however, we follow Maximov (17, pp. 251-4) and relegate succulents to a class by themselves, the relation of surface to volume loses much of its importance. The water reserve in "true xerophytes" has been shown to be of secondary significance (cf. Delf, 4, p. 117; Thoday, 30, pp. 592-3; Kamerling, 13; etc.). They have to maintain on the average a balance from day to day between transpiration and absorption. Three structural factors are of first importance in relation to such plants: (1) transpiring surface, (2) absorbing surface, (3) the resistances offered to the flow of water from one to the other. Any expression for estimating the structural xerophytism of a plant should involve all three<sup>1</sup>. Transpiring surface would then be measured in relation to the capacity of the plant to supply water to it. A practicable first approach to this would be to determine the leaf area in terms of unit-conducting capacity of the wood of the twig supplying them.

<sup>1</sup> For a fuller analysis see Huber (11).

It was with such considerations in view that in 1919, at my suggestion, R. D. Aitken undertook at Cape Town a comparison of the shoots of two trees, *Pinus pinaster*, with acicular leaves, and *Leucadendron argenteum*, with flat lanceolate leaves. Both are evergreen. The leaves of the latter, the well-known silver tree, which is very local on the slopes of Table Mountain, are 7 to 12 cm. long by  $1\frac{1}{2}$  to 3 cm. wide and are fairly numerous, clustered towards the ends of the branches. The stone pine leaves though longer are less than 2 mm. wide. Yet the total leaf surface exposed by twigs of the pine proved to be not far short of that of similar twigs of the silver tree. The averages for a number of twigs were respectively 1550 and 1150 sq. cm. per twig<sup>1</sup>.

The conductivity of the wood of the silver tree was greater than that of the pine, so that when the ratios of leaf area to conductivity were calculated figures of the same order of magnitude were obtained for both, or, in individual cases, much greater ratios for the pine.

Transpiration experiments also gave much greater rates for pine than silver tree. These experiments made with twigs cut some time before use, brought in a vasculum to the laboratory and set up in water with the usual precautions, were not regarded as wholly satisfactory. A method was needed by which a closer approximation to the actual transpiration of a twig before detachment from the tree could be obtained. Unfortunately Aitken's departure brought the work to a premature termination.

Since then Stocker (27) has estimated the surface area of the foliage of ericoid moorland and heath plants and was impressed by their "ausserordentlich Oberflächenvergrösserung, die durch die ausserordentlich grosse Anzahl, wenn auch kleiner, Einzelblättchen entsteht," especially in proportion to their root systems. Like Groom for Conifers (6), he correlates their xeromorphic structure with their large surface as complementary phenomena. Huber (10) has related transpiration to the conducting capacity of the wood in several trees, using Farmer's conductivity data (5), and has devised a promising method for obtaining a close approximation to the transpiration of intact twigs (12). He has also estimated, more accurately than Stocker, the surface exposed by some pinoid and ericoid types, among others, relative to their volume. From these and other researches it has become abundantly clear that the idea that small-leaved plants in general expose a small transpiring surface will not bear examination, and that, apart from desert succulents, plants with xeromorphic foliage are not characterised by a low rate of transpiration, but more often by a relatively high rate (Maximov, 17).

My own observations and experiments and Aitken's work led me between 1920 and 1922 to draw attention to certain functional aspects of microphylls (30; 31, pp. 62-3; 29).

<sup>1</sup> Groom (6) estimated the total leaf surface of certain Conifers and found it often much greater than for dicotyledonous trees of equal age. He based his calculations in part on data provided by von Höhnelt.

Farmer in 1918 had demonstrated the correlation between resistance to flow of water in the wood and xeromorphy of evergreens (5). It was a natural extension from this to expect that structural modifications tending to reduce resistances within the leaf itself might be as important for xerophytes as features leading to a reduction of transpiration.

Measurements made by me on sunflower leaves in 1908 had revealed that in dry sunny weather "the leaf shrinks more and sooner, and recovers more tardily, towards the tip than it does nearer the base" (33, p. 29). Yapp's work on *Spiraea* (38) showed that the parts of the leaf farthest from the main channels of supply were the most vulnerable and the first to shrivel in drought. In lobed leaves it is just these more vulnerable parts which are, so to speak, omitted. In the extreme cases of dissected leaves with narrow linear or filiform segments and of pinoid, ericoid and cupressoid leaves, no part of the mesophyll is more than a very short distance from the main channels of supply. The reduction of internal resistance is probably far more significant than reduction of surface, which is in fact often illusory. Maximov has recently advocated the same point of view (17, pp. 386-7).

Pursuing this line of thought in its application to the internal structure of the leaf, the centric type of leaf in which the palisade cells radiate directly from the central bundle may be regarded as reducing the resistance within the mesophyll itself to a minimum. The importance of this is illustrated by the distribution of suction pressure found by Ursprung and his collaborators in ivy leaves (34, 35), which indicates great resistance to lateral flow through the mesophyll. All those arrangements which Haberlandt (7, p. 280 *et seq.*) enumerates under his principle of expeditious translocation should be significant in this relation also.

In broad leaves the provision of a central plate of continuous "water tissue," or especially of tracheids, must very materially facilitate lateral spread of water from the veins to the bases of the palisade cells or cell rows. It may be doubted whether storage of water is in many cases a function of more than secondary importance (cf. Thoday, 30, p. 592), or even, in the absence of positive experimental evidence, whether it is subserved at all. In a case investigated by Miss S. Garabedian, that of *Mimetes lyrigera*, in which a group of so-called water-storage tracheids occurs near the tip of the leaf, no evidence could be obtained of the tracheids giving up their water, even when the water content of the leaf was reduced to a dangerously low level such as is rarely if ever reached in nature<sup>1</sup>. The conducting function of such tissues

<sup>1</sup> It is obviously necessary to draw a distinction between water storage and mere retention of water. Vacuolated cells retain water; in proportion to the extensibility of their walls they may store it. Thus all the living cells of succulent plants store water, more or less. Storage capacity is increased if the cells are capable of withstanding without injury the crumpling or folding of their walls. (Where, as in so many leaf succulents, *Mesembryanthemum* spp., etc., the old leaves shrivel completely, the whole of their water of course becomes available to the younger leaves; but the yielding of water is in this case irreversible. Cf. Delf, 4, p. 116.) The bellows-like



is recognised in the leaves of Gymnosperms by the term "accessory trans-fusion tissue." This term might usefully be applied in other cases also.

There is another effect of microphyllly which may be of some ecological and physiological significance. Small, narrow leaves are not aggregated into a continuous leaf mosaic. Light penetrates between them, directly or reflected from their rounded surfaces, and a proportion of it reaches leaves below un-filtered of photosynthetically active rays (31, p. 62; 32, p. 202)<sup>1</sup>. A greater

character of the cell walls of specialised water-storage tissues, as figured by **Haberlandt** in the leaves of *Peperomia trichocarpa* (7, p. 401, Fig. 159) and easily demonstrable in the South African species *P. retusa*, greatly extends the range of storage volume. These tissues yield water to the photosynthetic tissues. This ability to yield water to other tissues with more important functions entitles them to be regarded as water-storage tissues *par excellence*.

Tracheids, on the other hand, do not expand and contract osmotically, though if thin walled they might perhaps collapse reversibly under cohesion tension. Only by observations and experiments on living material can we determine how the tracheids behave during drought; but not for more than one or two cases is any evidence available. The positive observations of **Kny** and **Zimmermann** (14) on *Nepenthes* leaves and of **Rothert** (20) on the scattered tracheids in the pith of *Cephalotaxus koraiana* twigs can be placed against our negative result for *Mimetus*. With regard to *Nepenthes phyllamphora* in which the long "spiral cells" were observed to be full of water in the turgid leaf and to become emptied as it loses water, **Kny** and **Zimmermann** conclude that these elements serve "für eine Speicherung und möglichst gleichmässige Vertheilung des Wassers an das Assimilationsgewebe" (italics mine).

As regards the leaves of South African sclerophylls, should tracheids be emptied of water, it is difficult to conceive of them ever being filled again, as long as the dry season lasts; nor could the volume of water they contain be of real significance in relation to the seasonal transpiration.

It is worth notice that **Kny** and **Zimmermann** and also **E. Heinricher** (8), who appears to have been the first to use the term "Speicher-Tracheiden," associate together storage and distribution: e.g. **Heinricher**, "welche einerseits für die rasche Zufuhr, anderseits für die Speicherung des Wassers bestimmt sind" (note also the title of his paper). Similarly **Scheit** (22) thinks of the transfusion tracheids in Gymnosperm leaves as both storing water and extending the surface of contact between the conducting and assimilating tissues.

<sup>1</sup> Data on the reflection of light are rather meagre. It is clear from a comparison of green and golden or chlorotic leaves that much of the light is reflected after penetration from internal surfaces and, in the case of the green leaf, filtered by chlorophyll. The most recent data, those of **Shull** (24), refer only to the amount of light reflected perpendicularly by a horizontal leaf surface when uniformly and diffusely illuminated from all directions, as from the whole sky. For the upper surface of ordinary mature green leaves his figures vary from 3.5 to about 10 per cent. at  $\lambda$  6800 (for green light the values were of course higher) relative to the amount reflected under like conditions by a mat white surface (of magnesia). **Pokrowski** (18) obtained similar figures for 90° incidence. **Coblentz** (3), on the other hand, though he obtained low values for the reflectivity of leaves at 45° incidence compared with a plane mirror, yet when he used apparatus which integrated the diffuse reflection of light incident 90° on the surface obtained at  $\lambda$  6000 values varying from 22 to 27 per cent. of the incident energy. (Shull has, I think, misunderstood Coblentz's very brief particulars and confused the conditions of two sets of observations made by him with different apparatus.) At smaller angles of incidence the proportion of light reflected would be still greater. According to **Coblentz** (*l.c.*) the blackest deposit of soot, deposited on a metal plate from an acetylene flame, "viewed at grazing emergence has the appearance of a highly polished mirror of fairly high reflecting power." Shull's data illustrate the higher reflection from paler green leaves, from the under surface of most leaves, and especially from a canescent surface: the under surface of the leaf of *Populus alba* reflected half as much as the magnesium oxide surface used for comparison.

depth of foliage is therefore effectively illuminated, and it seems likely that the light may be utilised more fully and economically than by plants which interpose a continuous layer of foliage. Such a layer, as experiments by Willstätter and Stoll (37, p. 127) have shown, may diminish the photosynthetic power of the light to very low proportions, yet a large part of the light absorbed cannot be used productively because of the low percentage of carbon dioxide in the atmosphere. The more direct sunlight is diffused and distributed, the larger the proportion likely to be utilised in photosynthesis. It would be interesting to compare the productivity of plants of the two types to see whether the microphyllous plant can accumulate more dry matter in relation to the gross amount of light intercepted. From this point of view the total leaf area might be expressed in terms of the gross area of shadow cast by the plant.

There is an analogous contrast in South Africa, between the dark green leaves of the forest and the lighter green leaves of the open veld: the former with palisade tissue of narrow cells usually confined to the upper side of the leaf, the latter thicker, often more or less vertically placed, with deep palisade tissue on both sides of the leaf, mostly of wider cells. These cells are relatively transparent, allowing a proportion of the light to penetrate, diffused but qualitatively little altered, to deeper layers of tissue within the leaf (cf. 25, p. 127). There can be no doubt that narrowness of the palisade cells diminishes not only the amount of light that is reflected out of the leaf but also its penetration into the leaf.

Thus the plants with wider-celled, deeper palisade tissue probably secure the effective illumination of a large volume of cells with a larger absorbing surface. The extent of the internal surface is of considerable importance since the greater part of the resistance to diffusion is located there, gaseous diffusion being relatively rapid<sup>1</sup>. Moreover in heliophilous plants the entry of carbon

<sup>1</sup> Brown and Escombe (2, p. 277) calculated for *Helianthus annuus* from Sachs' highest figure for the rate of increase in dry weight that the concentration of carbon dioxide only falls 5 or 6 per cent. from the atmospheric air to the respiratory cavities during maximal assimilation in the open air. If a greater internal surface were to be supplied through the same epidermis, the concentration of carbon dioxide in the air bathing the internal surface would not be reduced in proportion to the increased extent of that surface unless the air spaces offered a resistance to diffusion of the same order of magnitude as that offered by walls and protoplasm, which is far from being the case: cf. the calculations made by Schroeder (23) and also by Romell (19) who, applying Bohr's work on the resistance to invasion at a water-air surface, calculates that the partial pressure of carbon dioxide falls, in an ivy leaf, between the respiratory cavity and the upper epidermis, at most by about 7 per cent. Schroeder's corresponding figure, which Romell criticises, was about 19 per cent.

Romell's calculations, if sound, lend additional support to Lundegårdh's emphasis of the ratio between cell surface and the mass of chloroplasts to be supplied (15). He found that sun plants gave a higher ratio than shade plants, i.e. their chloroplasts were not as densely aggregated. This feature will also mean that a larger proportion of the light will pass between the chloroplasts, hence less thorough filtering and greater transparency.

It may be suggested, in passing, that Lundegårdh's assimilation curves for sun leaves and perhaps also for shade leaves may be affected by variations in distribution of carbon dioxide and light within the leaf. It is conceivable that under some conditions carbon dioxide might be limiting in the upper layers and light intensity in lower layers of a leaf illuminated only from above.

dioxide is often facilitated by a relatively high stomatal frequency. Some experimental data on comparative rates of photosynthesis appear to support this view, but data directly applicable are meagre and such as they are require further analysis (see Stiles, 26, pp. 139-40).

The relative translucency of microphyllous foliage, while it may enable the plant to use a larger proportion of the incident energy in photosynthesis, has the consequence that the plant does not throw a dense shadow and is less effective in the struggle for light. Microphyllous plants are as a rule light-demanding plants and succumb in competition with forest types if the moisture conditions are sufficiently favourable. These absorb in the shade a maximum proportion of the light that reaches them, at a minimum expenditure of constructional material. Later they keep the light from others which may well be capable of using it more productively.

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# THE PLANT COMMUNITIES OF TABLE MOUNTAIN

## II. LIFE-FORM DOMINANCE AND SUCCESSION

By R. S. ADAMSON.

THE general features of the plant communities of Table Mountain have been described in a previous paper (1)<sup>1</sup>, where the outlines of their structure and their relations have been traced.

These communities are characterised by large and varied populations and generally by a striking absence of dominant species and of species of decided social habit. The lack of dominants is seen both in seral communities and often in the climax. While there are a few communities here which exhibit true dominance of one or a few species these are quite the exception, the majority having a mixed population. In spite, however, of the absence of dominance these communities have a definite physiognomy and can be readily distinguished from one another in the field, though the ordinary canons of description are not readily applied.

Since the floristic composition of a community must ultimately be its most important characteristic (cf. 6, 5, 7) an investigation was made with a view to finding some explanation of the apparent variability of the floras.

For special investigation a number of communities were selected on the north- and west-facing slopes of Table Mountain at an altitude of 300-360 m. (1000-1200 ft.). Communities from other parts were investigated for comparison and the results have been tested on a large number of examples scattered over a wide area. The selected communities were on a granite slope more or less covered by sandstone talus. The area taken for detailed study was restricted at first in order to limit the number of variable factors and to allow a readier comparison of different stages in succession. A study by purely statistical methods was made but did not give results that seemed to afford any clue to the peculiarities of these communities (cf. 2, 3, 5, 11, 19) and a broader basis of study was therefore employed.

The general method used was that of sample quadrats (20). A number of these were taken in a limited area of a definite community. In most cases the samples were scattered at random, but in some examples a definite plan was followed, the quadrats being arranged along straight lines. The results, however, did not show significant differences.

In the majority of cases quadrats 1 m. square were used, but for stages near the climax, where large shrubs are present, the size was increased to 2 m.

<sup>1</sup> Numbers in brackets refer to the list of literature at the end.

In the first cases examined fifty quadrats were employed, but owing to the amount of time and labour involved this was later reduced to twenty-five for each community. While some of the numerical features are obscured by the smaller number of samples, the general features seem equally well brought out (cf. 17, 24).

*Frequency.* This method brought out very clearly the rather large population and the uneven nature of the species distribution. The distribution or frequency was taken as a percentage and the results grouped in five divisions, 1-20, 21-40, 41-60, 61-80 and 81-100. These can be labelled A, B, C, D and E respectively for convenience (12, 14, 15). The results are found to show very small numbers for the higher groups and in most cases to fall from A to E with no rise in the highest set.

The following table gives some illustrative examples. (*Note.* In this and all subsequent tables percentages are given to the nearest whole number.)

Table I.

No. of sample	Total species	No. of quadrats	Species per quadrat	Frequency (%)				
				A	B	C	D	E
2	96	50	11	75	16	6	1	1
14	63	25	16	60	17	11	6	5
6	98	50	18	68	16	7	7	1
11	86	25	15	61	26	6	6	1
17	88	50	14	79	9	4	7	0
9	44	25	14	47	16	18	9	9

In the above table Nos. 2, 14 and 6 were on sandstone talus on the north slope. No. 2 was very near the climax, No. 14 an earlier phase and No. 6 a community two years after destruction by fire. Nos. 11 and 17 were on a granite soil on the western slope, 17 was near the climax and 11 an early regeneration stage. No. 9 is a community from the plateau at 670 m. (2200 ft.) and is introduced for comparison. This plateau community exhibits, in its frequency distribution, features more like those in other regions (cf. 15, 24).

These figures may easily be objected to on the ground that, with such extensive and unevenly distributed populations, the results will be influenced by the size and number of the samples and by other factors (cf. 2, 3, 12, 17, 19, etc.).

While it is not intended to lay any stress on these figures, some checks were made to test the degree of accuracy of the apparent representations (11). For example, in some communities fifty sample quadrats were made; of these twenty-five were scattered at random, and twenty-five were arranged equally spaced on straight lines. The figures for each set of twenty-five were calculated separately as well as those for the whole fifty. Further, the sample quadrats were grouped in pairs giving twenty-five samples of double the area. As would be expected, this grouping of the quadrats alters the frequency values, the numbers being raised in the higher groups.



Table II gives the results obtained by this treatment in two cases. In each A represents the twenty-five scattered quadrats and B the twenty-five in line.

Table II.

List	No. of quadrats	Total species	Frequency (%)				
			A	B	C	D	E
18	50	93	67	16	10	4	2
18 A	25	86	64	16	12	5	2
18 B	25	75	63	17	15	4	3
18	25	93	58	14	12	8	7
	(double)						
17	50	88	79	9	4	7	0
17 A	25	78	73	12	9	5	0
17 B	25	69	75	9	7	9	0
17	25	88	65	17	4	7	7
	(double)						

An examination of the figures so obtained shows a good degree of consistency for 1 m. quadrats, but a decided alteration when the size is doubled. Investigations have not been pursued on the effect of still further altering the size of the sample, as it was felt that these frequency figures by themselves were not giving results of a value at all compatible with the time and labour needed when dealing with this type of community. The agreement that is shown between the findings from twenty-five and from fifty quadrats was considered sufficiently close to enable the smaller number to be regarded as sufficiently adequate for sampling. As the scattered quadrats contained a larger number of species this arrangement was generally followed.

Apart from the size of the quadrat the results were found to vary considerably with the season at which the examination was made. These communities contain a considerable percentage of Geophytes and other plants with a short active season in the spring (1). The inclusion or exclusion of these plants has a noticeable effect on the distribution of the frequency classes. One example will be sufficient to illustrate this. In this example the lists were made in September and in January:

	Total	A	B	C	D	E
September	90	61	23	8	8	1
January	64	70	14	8	6	1

Since these temporarily active plants are rather numerous and as the figures show that most of them are not uniformly distributed, it was decided to take all the examples for comparative purposes in summer or winter and so to avoid the increased complication.

In any case the distribution of the frequency classes must be taken along with a consideration of the species composing them if real information is to be obtained. In many of these communities it is found that the species with the highest frequency indices are not those that would on other grounds be looked upon as most important in the community. To illustrate this the list

of those with an index of 80 or over (Class E) in the examples given in Table I is given below:

- Sample 2. *Cassytha ciliolata*, a parasite.  
,, 14. *Cassytha ciliolata*.  
      *Metalasia divergens*, a small undershrub.  
      *Adenandra uniflora*, a shrub with single shoots.  
,, 6. *Metalasia divergens*, a small undershrub.  
,, 11. *Euryops abrotanifolius*, an unbranched shrub.  
,, 17. None.

Not one of these plants could be looked upon as a species that determines the character of the community. These are only a few selected examples, but similar results have been found in the majority of the communities examined. In other words the species that give the distinctive features to the community are not those most generally distributed throughout its area.

A study of the frequency indices along with the numbers of individuals in the sample quadrats failed to show any local aggregations or grouping of species nor any clear cases of direct association of different species. There was nothing to indicate that the community was made up of a number of smaller assemblages either grouped or scattered through the whole area (cf. 8).

*Constancy.* The problem of "constancy" and of "exclusiveness" of the species (6, 5, 4, 8, 19, 21, etc.), has not been investigated to any extent and no attempt has been made to find the "minimum area" of the communities (5, 8, etc.). With communities possessing these large and varied populations such investigation would necessitate the examination of a large number of samples of different sizes. Further, the communities here form a mosaic of stages of regeneration after fire (1) and climax communities are rare, so that comparisons between really corresponding stages are by no means easy to make.

*Areal percentage.* The sample quadrats have been employed for the determination of the areal percentages (cf. 20). For this only species covering  $\frac{1}{32}$  (0.03125) or more of the sample quadrat were given a value. With this plan some rather striking figures were obtained, and these bring out even more clearly than do the frequency indices the uneven nature of the floristic distribution. The values of the areal percentages are very small. Out of fifteen communities studied six had no species showing a value of more than 10. In all together the maximum value was 24, which is by no means a high figure when compared with the more uniform communities of other regions (cf. 24).

*Life forms.* The species were divided into life-form groups according to the system of Raunkiaer (10, 23) which has the advantages of simplicity and is now very generally used. In classifying the plants an arbitrary distinction was made between micro- and nano-phanerophytes rather different from that used by the original author of the scheme. The two were separated in accordance with the layers in the community. There is a definite stratum of

plants about 0.25 to 0.75 m. in height which were treated as nanophanerophytes, while plants distinctly taller and forming an upper stratum were put in the other group.

Spectra based on these life forms have been given previously (1), but do not yield much information for the present problem. It was found necessary to subdivide the life-form groups, and again the system of Raunkiaer (10) was followed. This subdivision into leaf-size classes applies well to the phanerophytes and chamaephytes but does not take into account the hemicryptophytes and especially the Monocotyledons in this group. As Monocotyledons often play an important part in these communities an extension of the scheme of classes was made to cover some of the hemicryptophytes. In these communities the most important were plants with erect more or less leafless assimilating stems on the one hand, and on the other more or less tufted plants of grass habit. In taking these two as classes no systematic basis is used. The grass type includes many Cyperaceae and excludes such a true grass as *Ehrharta aphylla*. The assimilating stem type was made to include plants with very stiff erect leaves, e.g. several species of *Tetraria*. It includes the great majority of the Restionaceae.

*Analysis of communities.* While an analysis of a community on the basis of these life-form leaf-size classes involves a large number of divisions, no simpler plan seemed to work with the large varied populations. An actual example will serve to illustrate the features that seem to invite attention. The example selected is a community approaching the climax. It was on a granite soil, with some sandstone débris, on the west side of the mountain. The community was stratified: the uppermost stratum, composed of *Protea lepidocarpodendron*, was by no means continuous. The bushes were scattered all through and only occasionally formed groups. Between and below them was a lower stratum of shrubs and Monocotyledons, with still smaller plants forming an incomplete third layer.

Table III. List No. 18. 88 species.

Species	Frequency		Areal percentage	Quadrats		Average number per quadrat
	%	Frequency		%		
M. mic.	1	60	60	14.175	60	0.6
N. nano.	7	36	6	0.437	32	0.3
N. lepto.	15	250	19	9.0	100	2.4
N. cpd.	2	18	9	0.375	18	0.1
Ch. mic.	1	2	2	—	2	0.02
Ch. nano.	6	60	12	0.187	44	0.5
Ch. lepto.	12	106	10	0.5	74	1.1
Ch. cpd.	1	28	28	—	26	0.2
H. as. st.	9	286	36	6.875	100	2.8
H. gr.	10	200	22	0.93	98	2.0
Others	35	348	11	2.5	100	3.5

M. mic. = microphanerophyta microphylla; N. nano., N. lepto., N. cpd. = nanophanerophyta nanophylla, leptophylla, and with compound leaves; Ch. mic., Ch. nano., Ch. lepto., Ch. cpd. = chamaephyta microphylla, nanophylla, leptophylla, and with compound leaves; H. as. st., H. gr. = hemicryptophyta with assimilating stems, and with "grass habit."

This table brings out a number of points. The microphanerophytes are represented by a single species which shows an approach to dominance with a relatively high frequency index and a larger areal percentage than any of the other classes. This is an almost normal arrangement. It is in some of the other classes that the special features are seen. Of these only those with the larger values for the frequency index and areal percentage need be considered in detail, namely *N. nano.*, *N. lepto.*, *Ch. lepto.*, *H. as. st.* and *H. gr.* classes. Of these the *N. nano.*, *Ch. lepto.* and *H. gr.* classes appear at once as of less importance owing to the very low values for the areal percentages as compared with the others.

The *N. lepto.* and *H. as. st.* classes both have an appreciable areal percentage and a high total frequency value. Further, each class is represented in every quadrat, that is, the class has a frequency index of 100. The classes, however, are composed of a number of species, thirteen *N. lepto.* and eight *H. as. st.*, and the individual species have a much smaller frequency index and quite small areal percentages.

The class as a whole appears to form a definite part of the community structure though the individuals composing it are not grouped in any definite manner. The component species in the class seem to be interchangeable and able to replace one another without altering the characteristics of the community as a whole.

The species in such a class which exhibit this interchangeability are not necessarily allied systematically (cf. 8). In this case the members of the two classes are as follows:

<i>N. lepto.</i>		<i>H. as. st.</i>	
COMPOSITAE: Metalasia	1 sp.	CYPERACEAE: Tetraria	2 sp.
Stoebe	1 "	GRAMINEAE: Ehrharta	1 "
ERICACEAE: Erica	3 "	RESTIONACEAE: Leptocarpus	1 "
POLYGALACEAE: Muraltia	1 "	Restio	2 "
RHAMNACEAE: Phylica	2 "	Thamnochortus	1 "
ROSACEAE: Cliffortia	1 "	Willdenowia	1 "
RUBIACEAE: Anthospermum	1 "		
RUTACEAE: Diosma	1 "		
THYMELAEACEAE: Passerina	1 "		
Struthiola	1 "		

This is just one example which shows characteristics that can be seen equally well or even better in many others and especially in those communities from the earlier stages of development.

In the communities on the exposed slopes of Table Mountain the climax has an upper stratum made up of one or a very limited number of species. It is in the lower strata that the great variety and this ecological interchangeability is apparent. In the earlier stages of the sere, before the uppermost stratum is formed, the interchangeability seems a more general feature.

*Seral communities.* Table IV gives the analysis of three seral communities.

Table IV.

	Totals	%	Frequency	Frequency per species	Areal percentage
List 14.					
M. mic.	3	5	68	23	8.625
N. nano.	3	5	136	45	1.0
N. lept.	12	19	184	15	3.625
N. cpd.	1	2	12	12	—
Ch. mic.	—	—	—	—	—
Ch. nano.	4	6	40	10	2.375
Ch. lept.	12	19	360	30	7.75
Ch. cpd.	—	—	—	—	—
H. as. st.	8	13	428	53	19.625
H. gr.	6	9	128	21	0.25
Others	14	22	216	15	—
List 8.					
M. mic.	2	3	6	6	0.25
N. nano.	7	10	276	39	5.25
N. lept.	11	15	280	25	5.87
N. cpd.	1	1	64	64	0.25
Ch. mic.	1	1	16	16	0.25
Ch. nano.	8	11	144	18	6.0
Ch. lept.	8	11	412	51	6.37
Ch. cpd.	4	5	100	25	—
H. as. st.	8	11	196	24	6.625
H. gr.	7	10	212	30	2.87
Others	15	21	220	15	0.5
List 17.					
M. mic.	2	2	8	4	—
N. nano.	7	8	152	22	1.42
N. lept.	12	13	204	17	3.15
N. cpd.	1	1	38	38	—
Ch. mic.	1	1	32	32	1.37
Ch. nano.	7	8	132	19	1.62
Ch. lept.	14	15	222	16	0.12
Ch. cpd.	1	1	34	34	—
H. as. st.	11	12	324	29	28.22
H. gr.	16	17	410	26	7.75
Others	21	22	252	12	2.06

Of these three communities 14 and 8 belong to the same sere. They are also closely allied to the one analysed above. Both of these were on the north slope of the mountain on a soil with a considerable amount of sandstone débris. 14 is a more advanced stage though definitely further from the climax than 18 which was discussed above. In 14 the plants that will ultimately form the uppermost stratum are present but are of small size and do not yet in any way dominate the other bushes. 8 is an earlier phase, a stage in regeneration after a fire about three years previously. This community is scarcely stratified.

Table IV shows a number of interesting points. As compared with the previous list, 14 is a simpler community, as is shown by the less abundance of microphanerophytes. In the lower strata here there is a decided predominance of the *H. as. st.* class with eight species and a high average frequency and areal percentage. Of these eight species six are members of the Restionaceae and the other two are Cyperaceae. One or other of the plants occurs in every quadrat, though no individual has a frequency index over 76.

Along with these the *Ch. lepto.* class is the most prominent and exhibits similar features. These two classes and the *N. lepto.* class show an interchangeability of species.

As compared with the previous list the earlier stage of development and the more exposed situation are shown by the greater prominence of the smaller plants.

List 8 is a much earlier phase in the sere, a one-layered community, which shows a marked variability of flora from plot to plot. The life-form classes are more evenly distributed in numbers, in frequency indices, and in areal percentages. A larger number of classes show interchangeability, *N. nano.*, *N. lepto.*, *Ch. nano.*, and *H. as. st.* The greater variety of life form, no one class of which is definitely of more importance than others in the community, is a character of the earlier regeneration phases on these talus slopes. As succession proceeds certain classes become predominant, as was noticed in the other list.

The third community analysed in the table belongs to a quite separate sere. It is a regeneration stage after fire, two years previously, on the sandstone on a steep slope. The type of community is very characteristic for such soils and situations. The soil here is very poor in humus. In this community the *H. as. st.* class is much the most important. It has a much higher areal percentage than any of the others. This class shows the features of interchangeability very well. While the class is present in every quadrat the constituent species have neither high values for frequency index nor areal percentage. The most important are:

	Frequency	Areal percentage
<i>Restio cuspidatus</i>	98	10.68
<i>Restio filiformis</i>	66	7.18
<i>Thamnochortus dichotomus</i>	46	2.85
<i>Th. cernuus</i>	28	2.31
<i>Elegia juncea</i>	28	2.06
<i>Leptocarpus incurvatus</i>	14	0.37

Of these *Restio cuspidatus* often occurs in the form of isolated shoots.

This kind of community, which is practically dominated by a number of Restionaceous plants, is exceedingly characteristic of poor sandy soils where fires have been frequent. With recurrent fires it may be apparently stabilised, but if left undisturbed other life-form classes gradually assume increasing importance.

*Life-form dominance.* Some of the results that can be drawn from these analyses may now be considered. The interchangeability of species of a life-form class, which is apparent in varying degree in all of them, may best be taken as an expression of what may be termed "life-form dominance." Instead of one or a limited number of species being dominant, one or more life-form classes play the same part in the community, even though these classes are composed of a number of species which are not of necessity related taxonomically. This life-form dominance may be confined to a single life-form class,



but in these communities it is more often seen in a number of classes which together characterise the community.

As compared with species dominance, life-form dominance leads to more varied communities from the floristic standpoint and to less definitely fixed populations. In succession the passage from one stage to the next is not at all necessarily associated with a change in the dominant life form (cf. 25). The change often occurs through regroupings of the important classes; and a series of stages, each distinct in itself, may have the same general distribution of life forms. Again life-form dominance may at any stage pass into species dominance when one member of a class increases at the expense of the others.

*Succession.* Some examples may be given in illustration of some of these points. The following table shows two analyses from the same community, taken at an interval of two-and-a-half years. The community was one in course of regeneration after fire. The fire occurred three years before the first examination.

Table V.

	No. 8. Nov. 1927.				No. 20. May 1930.			
	Totals	%	Frequency per species	Areal percentage	Totals	%	Frequency per species	Areal percentage
M. mic.	2	3	6	0.25	1	1	12	—
N. nano.	7	10	39	5.25	9	14	27	2.87
N. lept.	11	15	25	5.87	10	15	20	5.75
N. cpd.	1	1	64	0.25	2	3	24	—
Ch. mic.	1	1	16	0.25	1	1	4	—
Ch. nano.	8	11	18	6.0	7	11	24	16.175
Ch. lept.	8	11	51	6.37	8	12	30	7.75
Ch. cpd.	4	5	25	—	4	6	19	—
H. as. st.	8	11	24	6.25	6	9	43	10.62
H. gr.	7	10	30	2.87	6	9	28	0.5
Others	15	21	15	0.5	12	18	20	0.5

Of these two lists the first shows the features already noted as characteristic of the earlier stages of regeneration; a number of the life-form classes are of about equal importance, and all these show interchangeability. In the later stage several differences are to be seen. These are not all, however, of the same importance.

The most marked and noteworthy are in the *Ch. nano.* and *H. as. st.* classes, smaller changes occur in *N. nano.*, *Ch. lept.* and *H. gr.* classes. The last of these is probably not significant, being due to the difference of season at which the lists were made. The slight decrease in the *N. nano.* class is due to the fact that several of these sprout from the base after fire (e.g. *Royena glabra*, *Montinia acris*) and spread over a considerable area: later they become restricted in area rather than in frequency. The decrease in the frequency of the *Ch. lept.* class is a characteristic of the development of the sere. The slight increase in the areal percentage in this class is almost wholly due to one species, *Metalsia divergens*, which has increased from 5.12 to 7.62.

The changes in the *Ch. nano.* and *H. as. st.* classes are, however, of much greater importance. In the former the increase is almost wholly in areal percentage; the number of species and the frequency index are the same in the two. The increased areal percentage is the result of the rapid spread of one species, *Helipterum gnaphaloides*, which has an increase in areal percentage of 5.5 to 16.0. The increase of this species is purely temporary. At the time of the second of the two examinations many of the plants were becoming straggling and already showing signs of having attained the limit of their activity. In all probability in another two years the amount of this species will be greatly reduced. The increase is a specific one and not a case of life-form dominance.

On the other hand, the *H. as. st.* class shows different features. The frequency index is much higher in the later stage and the areal percentage has increased by over 50 per cent. The total areal percentage of 10.6 is the sum of those of 6 species, only 1 of which has a figure exceeding 2.5. Almost all these species show a distinct increase as compared with the earlier stage. The component species of the class have low areal percentages and often rather low frequency indices but together they form an important part of the community, and, as a class, are present in every quadrat. This is a good case of life-form dominance with interchangeability. The actual figures for the species are:

	1927		1930	
	Frequency	Areal percentage	Frequency	Areal percentage
<i>Elegia juncea</i>	8	0.25	Not recorded	
<i>Restio cuspidatus</i>	60	—	44	0.125
<i>R. ferruginosus</i>	12	0.25	Not recorded	
<i>R. filiformis</i>	48	1.0	80	4.5
<i>Tetralaria compar</i>	20	1.375	24	0.75
<i>T. ustulata</i>	12	2.5	24	2.5
<i>Thamnochortus dichotomus</i>	12	0.5	30	1.875
<i>Willdenowia striata</i>	24	0.25	56	0.875

The comparison of these two stages in succession is sufficient to indicate that life-form dominance and interchangeability are not of universal occurrence. Under certain circumstances individual species may increase very greatly or even attain dominance. This gives a wide scope for local variations in the seres: advance may be caused by a life-form class or by a single member of it. Where one species of a class which comprises a number shows this sort of increase the mere arithmetical tabulation of the classes may quite obscure the true state of affairs. An example of this may be seen in some of the communities on clay soils derived from the granite. On such soils after fires the rhenosterbush (*Elytropappus rhinocerotis*) may attain true dominance. It forms, however, a temporary though prolonged stage, and gives way ultimately to other ericoid bushes. The following figures give the more numerous classes in an analysis of such a community in which the rhenosterbush is in course of being overcome.

Table VI.

	<i>N. nano.</i>	<i>N. lept.</i>	<i>Ch. nano.</i>	<i>H. as. st.</i>	<i>H. gr.</i>
Totals	2	10	4	5	4
Frequency	180	315	55	95	65
Frequency per species	90	31	14	19	16
Areal percentage	1.87	45.46	1.4	1.87	0.37

In this community the *N. lept.* class is evidently very much the most important. It contains more species than the others, has a high frequency index, and a large areal percentage. The figures might be taken as clearly indicating interchangeability, but a more careful examination shows quite other features. Firstly in this class three species account for practically the whole of the areal percentage of the class: *Erica imbricata* 29.3, *Blaeria ericoides* 8.7, and *Elytropappus rhinocerotis* 5.78. Of these three *Erica* and *Blaeria* act together, but they are competing with *Elytropappus* for dominance and in this example have together very nearly overcome it. Here the two stages succeeding one another in the sere are characterised by species of the same life-form class (cf. 25) and in each there is species dominance of the ordinary kind. Such cases are the exception in this region.

#### Plateau community.

Life-form dominance is not confined to the communities of the lower slopes. It also characterises those on the plateau. It was noted above that in these the distribution of the frequency classes was more of the expected kind. In the plateau communities the number of life-form classes which exhibit interchangeability is smaller as a rule.

The following table is based on a community on the lower plateau at an altitude of 670 m. (2200 ft.), on level ground with a humus soil. The community is a stage in the regeneration after fire, three years before.

Table VII. *Hemicryptophytic community on lower plateau.*

	Totals	%	Frequency	Frequency per species	Areal percentage
<i>N. nano.</i>	1	2	8	8	0.25
<i>N. lept.</i>	7	16	304	43	4.5
<i>N. cpd.</i>	1	2	4	4	—
<i>Ch. mic.</i>	1	2	12	12	—
<i>Ch. nano.</i>	1	2	4	4	—
<i>Ch. lept.</i>	4	9	140	35	1.25
<i>Ch. cpd.</i>	2	4	88	44	0.75
<i>H. as. st.</i>	5	11	300	60	38.5
<i>H. gr.</i>	7	16	212	30	14.75
Others	15	34	344	23	3.75

These figures show that this is essentially a hemicryptophytic community. In it the *H. as. st.*, *H. gr.* and to a less extent the *N. lept.* classes show the interchangeability resulting from life-form dominance. Each class is composed of several species which have small areal percentages. The numbers of species for which an individual areal percentage was assigned was *H. as. st.* 5, *H. gr.* 5, and *N. lept.* 3. These classes, however, take a large part in the make

up of the community. As development proceeds the *N. lepto.* class will increase in numbers and importance and ultimately attain dominance, though no single species can be described as a dominant in the ordinary sense.

### *Climax.*

While these features of interchangeability and life-form dominance might perhaps be expected in seral communities, in this region they can equally be demonstrated in the climax. On Table Mountain the climax community of the lower slopes has a rather uniform upper stratum, but the remainder of the community clearly shows the features referred to. On the plateau and in many other parts of the country this uniformity is not found in any of the strata of the climax.

Owing to destruction by fire, climax communities are rare on the slopes of Table Mountain and a complete study of a fully developed example has not been possible. In communities approaching the climax, life-form dominance was especially noticed in the *N. nano.* and *N. lepto.* classes which occur in every quadrat, have a high frequency index and considerable areal percentages. The classes comprise a number of species which individually have not very high frequency indices or other characters of dominants.

As an example of a climax community a study was made of one situated near Hermanus on the south coast of the mainland. This community was on a gentle slope facing south at about 60 m. (200 ft.) above sea-level. The community was complex, arranged in three strata. In this case 2 m. quadrats were employed. The analysis is given in the following table. The larger quadrats used somewhat alter the values of the figures as compared with the other tables quoted.

Table VIII. *Climax, community near Hermanus.*

	Totals	%	Frequency	Frequency per species	Areal percentage
M. mic.	2	3	64	32	10.25
M. nano.	3	5	140	47	15.25
M. lepto.	1	2	4	4	0.25
N. nano.	1	2	4	4	—
N. lepto.	15	23	308	20	11.25
N. cpd.	2	3	16	8	0.125
Ch. mic.	1	2	12	12	1.0
Ch. nano.	3	5	56	19	1.625
Ch. lepto.	7	11	112	16	0.5
Ch. cpd.	1	2	8	8	—
H. as. st.	7	11	248	35	19.25
H. gr.	7	11	148	21	1.5
All others	15	25	112	7	—

A mere glance at these figures will bring out one feature of difference between this and the previous lists: the areal percentages are much less evenly distributed among the life-form classes. If the microphanerophytes which form the uppermost stratum are grouped together, only three classes have appreciable values.

In a complex community of this kind it will be most convenient to treat the strata separately. The uppermost is not a complete layer, in fact it only occupies about a third to a quarter of the whole community. This stratum is made up of six species, of which *Leucadendron salignum* is much more abundant than the others. While no one of these six plants has a frequency index of over 80, one or other of them is present in every quadrat. The actual figures for these species for frequency and areal percentage are:

	Frequency	Areal percentage
<i>Leucadendron salignum</i>	80	9.25
<i>Mimetes lyrigera</i>	36	4.875
<i>Protea longifolia</i>	32	5.25
<i>Pr. mellifera</i>	32	5.25
<i>Aulax cneorifolia</i>	24	1.125
<i>Erica sp.</i>	4	0.25
Total		26.0

These six species together form the uppermost stratum and all seem to play an almost equally important part in the community.

The second stratum is for the most part made up of the *N. lepto.* and *H. as. st.* classes. The former are the more numerous in species, but the latter have the larger areal percentage. In the *N. lepto.* class there are fifteen species, one or more of which is present on every quadrat but of which only one has a frequency index over 48. The total areal percentage is 11.25 which is made up of *Stoebe fusca* 5.75 and eight others with a combined total of 5.5. The remaining species in the class occur as isolated individuals. In these dense communities of the more advanced stages of the sere many of the plants of this class develop a characteristic form with a single elongated stem, which is either unbranched or only produces branches above the general level of the vegetation. Such plants may be individually frequent and have very small areal percentages and little effect in limiting the growth of other plants. Among plants of this community which have this habit are the following:

	Frequency	Areal percentage
<i>Anthospermum aethiopicum</i>	24	—
<i>Phaenocoma prolifera</i>	24	0.625
<i>Erica sp.</i>	8	0.25
<i>Podalyria sp.</i>	4	—
<i>Metalasia muricata</i>	20	—
(not always this habit)		

The *H. as. st.* class shows the characteristics of class dominance perhaps even more clearly. This class is present in every quadrat, but the frequency indices of the component species are not as a rule high. The actual figures are:

	Frequency	Areal percentage
<i>Restio cuspidatus</i>	80	4.25
<i>Leptocarpus asper</i>	60	5.875
<i>Thamnochortus dichotomus</i>	48	0.375
<i>Restio filiformis</i>	28	4.75
<i>Hypolaena digitata</i>	16	4.0
<i>Elegia sp.</i>	12	—
<i>Tetraria circinalis</i>	4	—

In this class four species are of especial importance in the community while the others are thinly scattered. These four appear to be able to replace one another. *Restio cuspidatus*, which has a higher frequency index than any other, has a less social habit and often occurs as isolated stems.

These two classes, *N. lepto.* and *H. as. st.*, make up the bulk of the second stratum, other life-form classes being much less abundant and less important.

The third stratum is not continuous or uniform. Some of the plants composing it are true shade plants growing under the cover of the larger ones, while others are confined to spaces between them. The constituent species show a variety of life forms and have generally low values for the frequency index and areal percentage.

### *Comparison of different localities.*

The examples so far treated have all been regarded from the standpoint of single communities. From them the principle of life-form dominance has been drawn. When corresponding communities from different localities are compared, even when the localities are separated from one another geographically by quite small distances, the diversity of species resulting from this feature becomes very marked. While the life-form spectra are identical the floristic composition is often very different indeed. Many of the species of the south-western portion of the Cape region have an extremely restricted geographical range (cf. 22), but in spite of this the general physiognomy of the communities is very uniform. As an example the shrubs of the uppermost stratum of the climax may be selected. On the lower slopes of the north and west sides of Table Mountain *Protea lepidocarpodendron* is the dominant; on the east side this is replaced by *Protea incompta*; in the southern parts of the peninsula *Mimetes hartogii* and *Leucospermum conocarpum* are present; corresponding communities on the opposite side of the Cape Flats are dominated by *Protea neriifolia*, *Pr. longifolia*, and *Leucadendron* spp. An example from slightly further east has been given already. The dissimilarity in flora is by

Table IX. *Comparison of climax communities.*

	Table Mountain		Common	Hermanus	Also on Table Mountain
	East side	West side			
M. mic.	3	2	1	2	0
M. lepto.	1	0	0	1	0
M. nano.	—	—	—	3	0
N. mic.	2	1	1	0	0
N. nano.	10	12	4	1	0
N. lepto.	12	19	8	15	4
N. cpd.	7	3	2	2	1
Ch. mic.	1	1	0	1	0
Ch. nano.	10	10	4	3	1
Ch. lepto.	2	4	0	7	2
Ch. cpd.	2	1	1	1	0
H. as. st.	4	4	1	7	2
H. gr.	5	8	3	7	3
Others	32	29	8	15	4
Totals	91	94	33	65	17



no means confined to the top stratum alone. As an example the life-form spectra of three climax communities are given, two from Table Mountain, one on the west side and the other on the east, together with that from Hermanus already noted.

Even without further analysis these figures are expressive. The number of species common to the two communities on Table Mountain is by no means large and the species common to the one at Hermanus and these two combined very few indeed. Yet there is not the least doubt about the very close relationship of the three communities.

#### GENERAL.

Life-form dominance, with its interchangeability of species, though such a distinct feature of these communities, is not by any means confined to them. The phenomenon can be seen in the grasslands of many regions, at any rate as far as the dominant grasses are concerned (cf. 7). Again in the forests of the tropics and the warmer regions of the earth life-form dominance exists among the trees. In such cases, however, one life-form class has attained complete dominance and this class alone shows the interchangeability of species. On the other hand, in the communities in this region several life-form classes are about equally developed and no one attains real dominance over the others. In the stratified communities each stratum shows this interchangeability of species.

Little definite information is at present available as to the causes underlying life-form dominance, though much speculation is possible. The species composing the communities on Table Mountain are characterised by an absence of distinct social growth. Even the hemicryptophytes merely form small tufts of very limited extent. This absence of social growth may be correlated with the prevailing climatic conditions, at least in part. The prolonged dry period in the summer may be looked upon as adverse to vegetative multiplication.

Another reason for this life-form dominance has been put forward: that it is one of the characteristics of a very old, long-established flora. A flora which has occupied a region for long periods of time, essentially undisturbed, would contain a large number of plants that have become adjusted to the conditions. Where many such occur, more or less equally adjusted, life-form dominance is the result. The floras which have received the most attention in intensive work, the European and the North American, are relatively very recent as compared with the Cape flora. It is not, however, my purpose at present to enter into any discussion of these or other views as to the origin of the phenomena. All that is desired is to demonstrate the existence and importance of life-form dominance.

The recognition of this feature should help to explain some of the difficulties that have been encountered in attempting to describe and classify the

communities of the warmer regions and the tropics in accordance with schemes based on the communities of temperate climates. The difficulty has been partly one of description in short form and partly one of definition. While the definition of an "Association" agreed to at the International Congress in 1910 is so general that it would easily cover communities with life-form dominance (9), in practice many writers on the nomenclature of vegetation have given definitions that either directly or indirectly imply *species dominance* (cf. 7, 8, 25).

#### SUMMARY.

The plant communities on Table Mountain have large and varied populations. The individual species are in most cases not evenly distributed through the area of the community.

Detailed examination by the sample quadrat method was undertaken on a number of communities. The frequency and areal percentages were determined. The species were classified in accordance with Raunkiaer's life-form and leaf-size classes, the latter being extended to include some of the hemicryptophytes.

Analysis of communities on this basis shows that the life-form classes often behave as units in the construction of the vegetation, the component species of a class being to a large extent interchangeable. There is *life-form dominance* rather than *species dominance*.

In most of the communities no one class becomes dominant: the life-form dominance is shared by two or more classes.

Examination of stages in succession shows that development may proceed by rearrangement of the proportions of the classes, or by a preponderance of one, or by one or more species in a class becoming increasingly abundant.

In stratified communities each stratum shows the same features. The interchangeability of species is also shown by comparison of similar communities from different localities.

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# PRELIMINARY OBSERVATIONS ON SCOTTISH BEECHWOODS (*continued*)

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(*With seven Figures in the Text.*)

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## PART II. THE STRUCTURE AND DEVELOPMENT OF WOODY COMMUNITIES ON HEATH IN THE NEIGHBOURHOOD OF ABERDEEN.

## CONIFER WOODLAND TYPES ON DEESIDE.

THE prevailing vegetation type in north-east Scotland is heath, superficially uniform in physiognomy but varying in its soil conditions, as the different rates of growth of planted pinewood show. It was planned to use this varying behaviour of the pine and the subsidiary vegetation of the pinewoods as a jumping-off ground for the attack upon the heath itself, or upon other communities of this area. This work had to be discontinued, but a flying survey of lower Deeside reveals the existence of at least three major types of pinewoods (pure or mixed, mainly with larch) named after the species characterising the different stages in the life history of the woodland.

*Type 1. Oxalis-Anemone-Rubus woods.*

*Type 2. Deschampsia-Vaccinium woods.*

*Type 3. Mossy Erica cinerea woods.*

Woods dominated by *Pteridium* also occur and appear to belong to a type coming between 1 and 2.

Each type may be considered the centre of a group, the outermost individuals of which show approaches not only to the next in the above series but to communities of wetter soils.

*Type 1.* Woods of this type grow on loamy soil with an average depth of about 2 ft. (60 cm.) and with little or no visible bleached layer. The soil is well suited for arable cultivation, hence examples of Type 1 woods are few in number. Pine and larch grow well, the former often much damaged by squirrels, the latter relatively free from canker (*Dasyscypha calycina*) and reaching an average height of 74 ft. (22.5 m.) in 71 years. Data for the pine were not obtained but the height is less than that of the larch.

In the life history of the even-aged planted wood an *Oxalis-Anemone* stage is followed by one of *Rubus fruticosus* (agg.). A variety of this with *Vaccinium myrtillus* (apparently indicating an approach to Type 2) instead of *Rubus*, is also found. Examples of this variety come into the areas to be described later and are there referred to as Type 1.

*Beech grows well and spreads freely.*

*Type 2.* Woods of this type are common on soils showing a definite but often not very thick bleached horizon, and at a depth of approximately 15 ins. (37.5 cm.) below the mineral soil surface either an iron pan or more commonly a hard compact matrix of glacial till which holds up tree-root penetration. There are several varieties reaching out towards Types 1 and 3, but the most frequent shows a *Deschampsia flexuosa* stage followed by one of *Vaccinium myrtillus*. Neither pine nor larch grows so well here, the pine averaging 60 ft. (18 m.), the larch 65 ft. (19.5 m.) at 104 years.

*Beech* invades woodlands of this type but its growth is not so good and its regeneration less dense.

Type 3. Infertile, porous fluvio-glacial sands with well-marked bleached and illuvial horizons bear conifer woods of pine and larch: the pine at 63 years is 55 ft. high.

A mossy carpet, mainly of *Hylocomium splendens* and *Hypnum schreberi*, precedes a stage with *Erica cinerea* dominant. Varieties approaching Type 2 include *Deschampsia* and *Vaccinium* in the ground flora.

*Beech* does not occur in the examples seen<sup>1</sup>.

The following account deals mainly with the plant communities of Type 2: specific reference is made to those of Type 1.

#### THE VEGETATION OF FOUR AREAS NEAR ABERDEEN.

##### *Early history.*

The woody vegetation of four areas (Part I, Fig. 1, p. 152: and Figs. 1, 2, 3, pp. 324-326) in the vicinity of Aberdeen has been investigated in some detail to find out the relationship of the different plant communities and the place of beech in them. Two and perhaps three of these areas are included within the bounds of the ancient Forest of Stocket, of whose constitution we have no record, but "there is good reason for the belief that the indigenous trees of the vicinity of Aberdeen were practically destroyed, as the accounts of travellers in the eighteenth century agree in representing the east of Scotland as almost devoid of trees (22)." Instead the countryside is referred to as "barren lyke, the hills craigy, the plains full of marreshes and mosses, the feildes covered with heather or peeble stons, the corne feildes mixt with thes bot few"; "marshes and great stones," "foul moors," "heath and moor" are descriptions applied to it about the middle of the eighteenth century (23). The account of Keith is valuable. Writing of the parishes including Old and New Aberdeen he states that of the 5000 acres "little more than 500 acres, within 3 miles of Aberdeen, either were arable or could be cultivated by the plough. Above 3000 acres constituted a barren zone, of rough and broken ground covered with heath and large masses of granite." This granite was shipped for building and paving stone and partly compensated the expense of trenching the ground prior to growing crops. By 1814 "above 3000 acres have been trenched within 3 miles of Aberdeen; and many of the operators having carried their knowledge of the art into the interior districts of the county, probably not less than 20,000 acres in all, have, by a more or less perfect system of trenching, been added to the cultivated land of Aberdeenshire<sup>2</sup>."

Most of the land in the neighbourhood is now under cultivation, and it is exceedingly unlikely that in what remains untilled there is seen an exact

<sup>1</sup> At Darnaway in Morayshire, however, on fluvio-glacial gravel, beech grows well, reproduces freely and is replacing the oakwood planted in 1824.

<sup>2</sup> Keith in Sinclair's *General Report of Scotland*, 2, 396, 1814.



picture of the primeval conditions. The peats are cut and "mosses" exhausted, the heath lands burned over and open to grazing and plantations have been made. It is difficult if not impossible to find anywhere a piece of ground which one could call "natural" in the sense that it presents a vegetation not affected by man and his activities. And what is true in this neighbourhood is applicable to the major part of Scotland, including the higher ground as well. This ought to be kept in mind when the permanency of the beech and its status in the vegetation is under review.

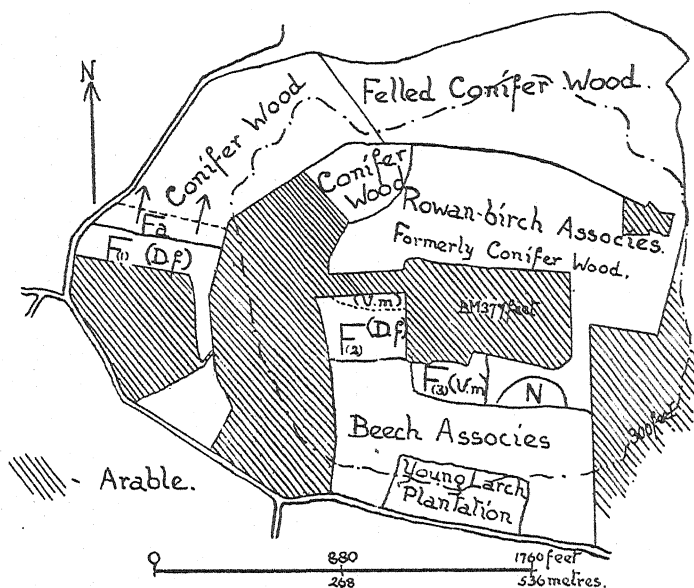


FIG. 1. *Fintray*. The woodlands occupy the slopes of a hill whose summit is near the centre of the figure. On the north and north-west sides conifer plantations occupy the lower slopes: the higher ground formerly carried a conifer crop, but now bears a rowan-birch associates. Adult beechwood grows on ridged soil at  $F_{(1)}$ ,  $F_{(2)}$ ,  $F_{(3)}$ , with *Deschampsia flexuosa* (*D.f.*) and *Vaccinium myrtillus* (*V.m.*) dominant in the ground vegetation where so indicated. Beech invasion of the coniferwood gives rise to the beech associates ( $F_a$ ). A beech associates, with relicts of a rowan-birch associates, both showing the rotting stumps of conifers, occupies the south-facing slope. At *N* a beech consociation nucleus is established, with birchwood forming a fringe marginal to it on the north side. The woodlands on the south-facing slope belong to Type 1.

### *Geology and soil.*

The woodlands described grow on glacial till overlying metamorphic and granitic rocks. Over much of the area the soil has apparently remained undisturbed. The surface is strewn with boulders, but the number and size of these are often obscured by the growth of plants and by the humus formed from them. Besides the boulders which lie on the surface, many others are completely embedded in the grey and coffee-brown horizons of the soil

profile, but below these horizons the stones are few in number and are found in a soil of open texture, which rests upon the compacted boulder clay. This concentration of boulders at or near the surface may be attributed to the washing away of the smaller soil fragments by glacial water. It is quite obvious that ordinary tillage operations could not be carried out until these boulders were removed, and it is considered safe to assume that a boulder-strewn soil of the kind depicted has never been cultivated.

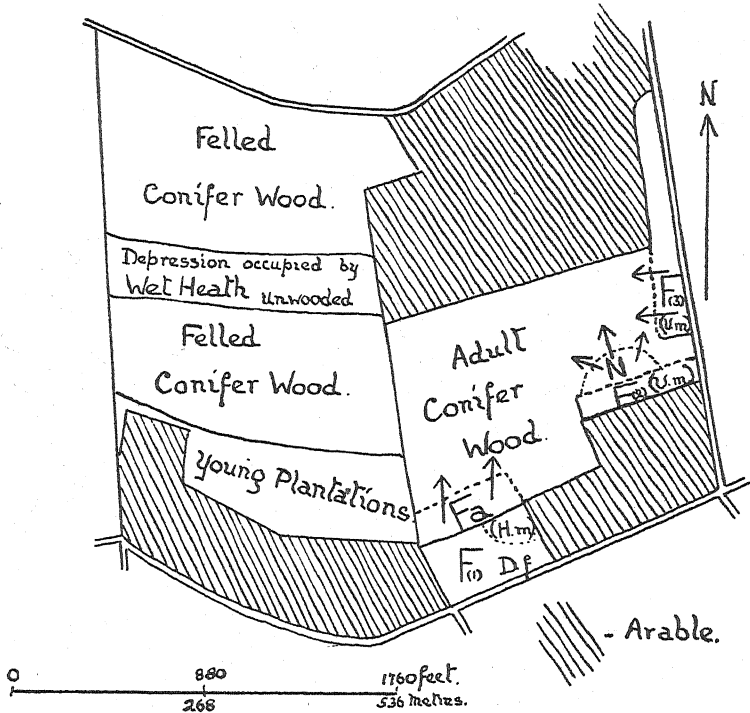


FIG. 2. *Countesswells*. Planted beechwood ( $F_{(1)}$ ) occupies ridged soil on a south-facing slope. The ground vegetation is dominated by *Deschampsia flexuosa* (D.f.), *Holcus mollis* (H.m.) replacing it in the north-east corner. On the higher flat ground behind is an adult coniferwood with belts of pure beech at  $F_{(2)}$  and  $F_{(3)}$  (*Vaccinium myrtillus* (V.m.) dominant). Behind  $F_{(1)}$ , beech invasion gives rise to a beech associates ( $Fa.$ ). Behind  $F_{(2)}$  a beech consociation nucleus (N) is established. The arrows indicate the direction of beech invasion.

The question then arises, do these wooded areas grow on soils considered unfit for arable cultivation? The chief possible causes of unfitness would seem to be unsuitable topography, difficulties connected with the removal of drainage water and of boulders, and poverty of the soil in nutrients. Wooded stony slopes unsuitable for tillage are found, but form a small part of the total wooded area. Further, none of the woodlands grow on a soil which presents serious obstacles to drainage or to the removal of drainage water; in fact some of them are intersected by a series of open drains, most of which

are now neglected. But unwooded wet heaths are to-day found in shallow basins which present obvious difficulties to the removal of the drainage water, and there is no evidence that these were ever planted. Again, while there is no definite evidence to prove that the wooded areas contain more or larger

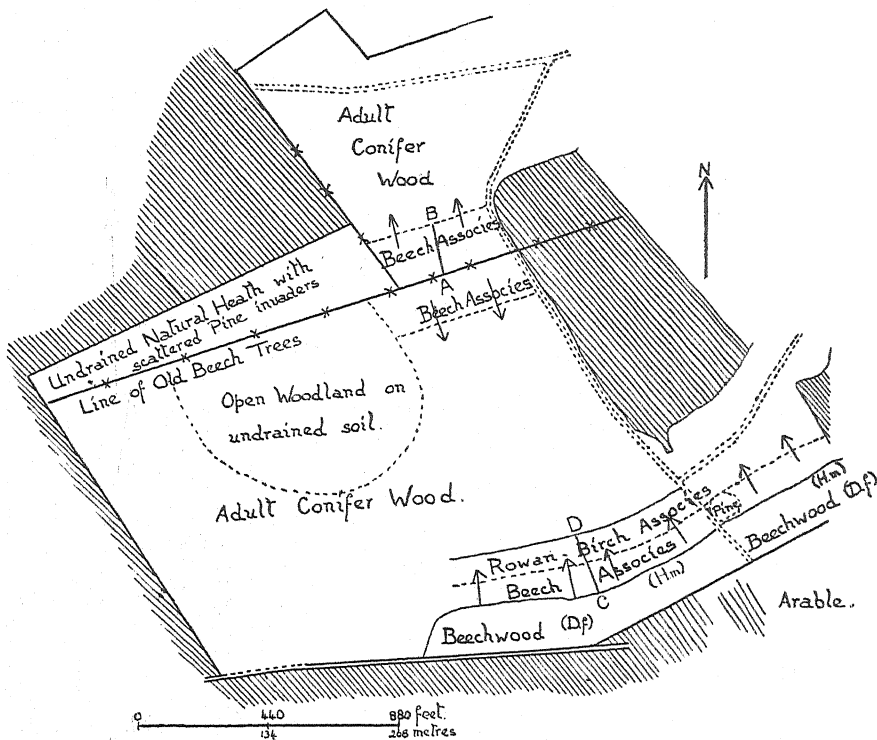


FIG. 3. *Hazelhead*. The coniferwood occupies uneven ground. The parts naturally or artificially drained bear denser woodland: the undrained part open woodland. Along the north-west margin runs a strip of undrained *Calluna*-heath with scattered pine invaders. Here are found heaps of boulders dumped during the clearing of the adjoining arable fields. A line of old beeches (x—x—x) of pioneer form runs alongside a dilapidated dyke marking the boundary between heath and woodland and continues eastwards through the coniferwood and between the arable fields beyond. Where the beech divides the coniferwood, free invasion on either side has taken place and a beech associes appeared. Along part of the southern margin of the coniferwood is a belt of beech planted on ridged soil. Behind the beech belt the conifers have been removed and the subseral rowan-birch associes has been invaded by beech and given rise to the beech associes. The transects (Figs. 6 and 7) are made along the lines AB and CD. The arrows show the direction of beech invasion.

boulders than the adjacent arable ground, the descriptions of the intake of heath plainly show that the "appearance of the surface of the muir was rather uninviting; for although, on different parts of it, traces of the old mode of culture by baulk and rig were apparent its general aspect was characterised by short stunted heath, in many places thickly studded with stones, and

with tumuli of stones and earth, indicating scenes of former bloodshed, with here and there boggy places interspersed. Its general appearance would not have led even an experienced person to expect anything like the uniform continuous extent of good soil, which the operations have since made apparent; and it was evidently much too rugged for the plough (4)." The boulders were used for building the farm houses and steadings, the stone dykes round fields and the surplus was got rid of in "consumption dykes"—all these exist as evidence of the abundance of boulders cleared from the ground. Further the straight alignment of the boundaries between woods and arable fields shows that discrimination between irregularly distributed cultivable and non-cultivable soils was not exercised and in fact on the Countesswells Estate part of one (Type 1) woodland adjoins arable soil stated by Sir S. J. Gammell to be the best on his estate. Finally the process of clearing continued after some of the present woodlands had been established, and in fact Stocket Moor itself was not brought under cultivation until about 1880.

For these reasons it is believed that the soil of the woodlands investigated does not differ materially from the original condition of that now under the plough, and by similar treatment could be brought into the same high state of cultivation as now exists.

Locally the soil is ridged, the width of the ridges from crest to crest being about 30 ft. (9 m.). Here there are no boulders or very few. This was the old method of cultivation and was primarily one of drainage. Where it is found the assumption is made that the soil was at one time under the plough but was later planted. In one example the boulders have not been carried off the ground but collected in the furrows and left there. Clearance of the ground unaccompanied by ridging is found but is rare. In all four localities practically the whole of the ridged soil is now occupied by beech.

#### *Chemical composition.*

No chemical analysis of the soil or of the different soil strata of the woodlands has yet been made, but the following conclusions from chemical analysis of the physical fractions of an arable soil are of interest. The sample was taken to a depth of 9 in. (22.5 cm.) from the farm of Craibstone (6 miles north-west of Aberdeen) whose woodland adjuncts grow on a soil similar to those under consideration.

"The Craibstone soil...is composed largely of particles which have not undergone profound chemical weathering, but consists of the original granite minerals mechanically ground with only comparatively superficial chemical alteration. The coarser particles which form so large a part of this soil contain great stores of lime in particular, and also of other bases such as potash, soda, and magnesia (7)." There is no free calcium carbonate (p. 460). This land under tillage forms a fertile soil and for the reasons given we may consider the results quoted generally applicable to the soils under woodland.

*Soil profile (Fig. 4 A).*

The soil is of the podsol type, but the horizons are not well differentiated. Thirty-nine diggings yielded the following data (averages, with extremes in brackets) respecting the thickness of the different layers:

Raw humus—9.5 (2.5–17.5) cm.

Grey layer—6.3 (0.6–15) cm.

Coffee-brown layer—4.8 (1.3–13.8) cm.

Humus-iron pan—weak, present in about 50 per cent. of the examples.

Rust-coloured layer—27.3 (12.5–48.8) cm.

Pan—iron pan present in about 10 per cent. of the examples.

At 37.3 cm.—unweathered and consolidated glacial till.

*Raw humus* is everywhere present and its depth and composition vary. It is often distinctly layered, the humus of one kind of plant resting on the humus of another, so that it is possible to trace the major outlines of the plant succession. Below the raw humus proper—and included in the above measurements—there is frequently found a layer of black amorphous peat resting immediately on the mineral soil.

*Grey layer.* This is visible in thirty-six out of thirty-nine of the soils examined, but in some cases it is very thin although quite distinct in the smallest thickness recorded. In no case has the bleaching progressed so far as to leave this layer white as seen in the poor soils of the Lower Greensand in Sussex, and the grey colour is often obscured by the infiltration of black humus from above. On drying and exposure to the air this layer becomes much lighter in colour and powdery to the touch.

*Coffee-brown layer.* This layer is found in twenty-seven out of the thirty-nine soils examined, and varies considerably in thickness and shade of brown, but is a somewhat consolidated layer coming away in chunks under lateral pressure of the spade. On the lower side it sometimes grades, when the pan is absent, into the rust-coloured layer and then an arbitrary measurement of its depth is made.

*Humus-iron pan.* In about one-half of the profiles a weak and easily disintegrated pan about 3 mm. thick is discernible either under the grey layer or the coffee-brown layer. Occasionally in the same digging one finds either a coffee-brown layer or a pan. Roots are stopped by it locally, but it seems to have little effect on root penetration generally. This applies particularly to tree roots, whose descent was never observed to be interfered with by this layer.

*Rust-coloured layer.* This layer varies much in thickness, colour and texture. It is generally a sandy loam and reddish in colour, due to the deposition of iron.

*Pan.* In a few cases the roots of trees are stopped suddenly by an iron pan about 3 mm. thick.

*Unweathered glacial till.* In most cases the change is abrupt from the rust-coloured layer to the grey, compact, unweathered till, itself almost as effective

as pan in preventing root penetration. Locally the soil is more sandy and there is little change in texture downwards, but the colour change and the slight difference in compactness are used as a guide to the depth of the rust-coloured layer<sup>1</sup>.

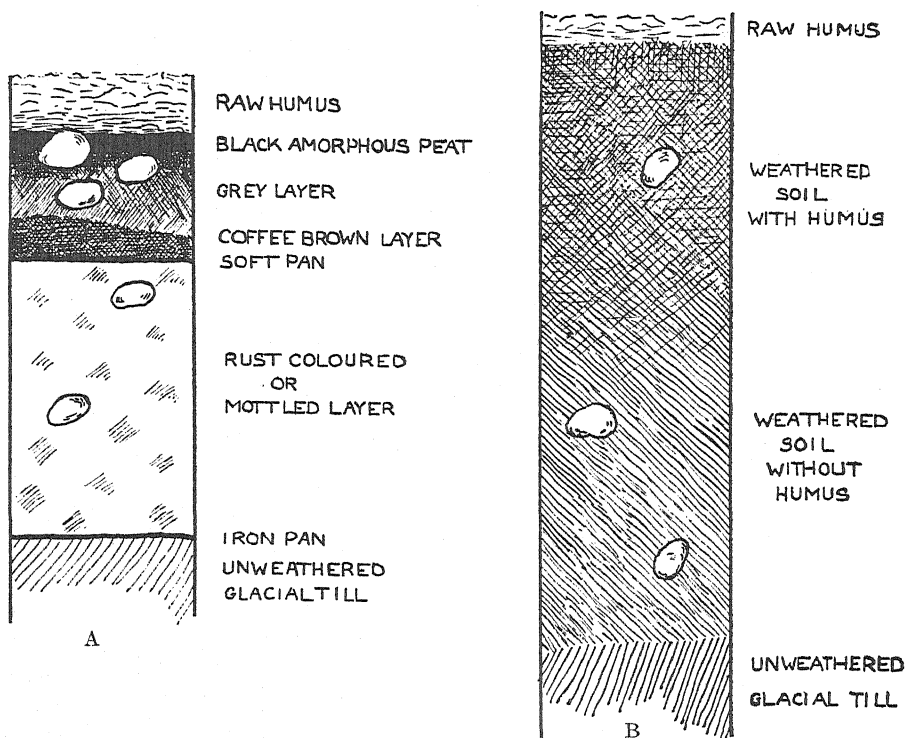


FIG. 4. A, Typical soil profile of the heathwoods (Type 2) showing distinct podsolisation; B, of Type 1 woods with no visible illuvial horizon but occasionally showing slight bleaching of the surface mineral soil.

### Soil depth.

The volume of soil available for root exploitation is determined by the depth at which the consolidated soil is found. The average depth (measured from the surface of the mineral soil) is only 15 in. (37.5 cm.). This is of great direct importance to tree growth, inasmuch as deep-rooting trees like larch, pine and oak do not have a soil depth adequate to normal root development. It is important indirectly, as interference with drainage sets up conditions hostile to the normal functioning of roots. In winter the ground may become sodden and in late summer the grey layer under the pine and the mat of *Deschampsia flexuosa* is found in an extremely dry powdery condition.

<sup>1</sup> In some profiles there is definite evidence of bleaching in badly drained soils due to the action of underground water. The "rust coloured" layer is then light in colour. Soils of this type are classed as "podsol-glei" soils and if they bear pines at all, these are of very poor growth.



*Soil acidity.*

A well-marked acidity gradient is brought out by the following averages (extremes in brackets) from twenty diggings:

Raw humus	...	...	...	pH 3.9	(3.6-4.2)
Black peat	...	...	...	4.0	(3.6-4.2)
Grey layer	...	...	...	4.0	(3.6-4.3)
Coffee-brown layer	...	...	...	4.2	(4.0-4.6)
Rust-coloured layer	...	...	...	4.75	(4.6-5.0)
Parent glacial till	...	...	...	4.8	(4.6-5.0)

These data are very similar to those obtained by Hesselman (8) from the heathy woods of Scandinavia.

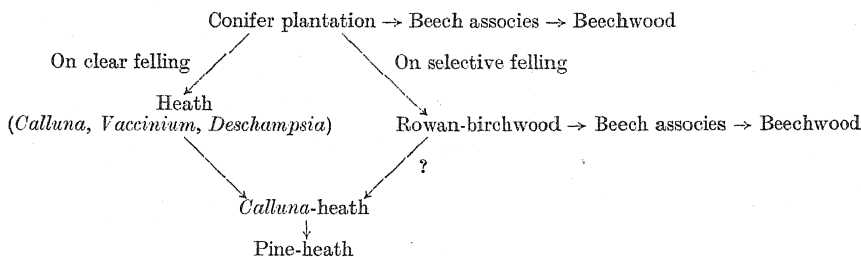
On the south-facing slope of the Fintray area (Fig. 1) and in a woodland about 0.5 mile west of Countesswells House, plant communities belonging to Type 1 are found. In the soil profile (Fig. 4 B) there is no visible succession of horizontal layers, although a soupçon of a grey layer is occasionally met with. The humus (2.1 in. i.e. 5.3 cm. thick) disintegrates more rapidly and is more friable, and beneath it there is a loamy soil whose upper layers are darkened by humus, the distinctive soil colour—yellow to reddish brown—being apparent below. The average depth of mineral soil in seven diggings was 22 in. (55 cm.) and this overlies hard compact glacial till. In this soil earthworms are much more frequent.

#### THE PLANT COMMUNITIES: THEIR RELATIONSHIP AND GENERAL DESCRIPTION.

The whole extent of man's influence on the vegetation cannot be judged until we know more about the primeval vegetation. This seems to have been heath with peat in the wetter parts, but of the tree species, their size and frequency, we have no certain information. But from the historical notes given and evidence adduced later the belief is entertained that in a general way the neighbourhood of Aberdeen was occupied by heath, studded with trees of pine, birch and rowan, varying in relative frequency and density from place to place but with pine the most generally abundant and prominent. The existing coniferwoods are planted, apparently with no soil preparation except for the cutting of shallow drains, most of which are now neglected. Pine and larch form the bulk of the plantations with spruce and silver fir sparsely distributed, and these trees by their selective effect have altered the relative frequencies of the pre-existing flora. Exploitation of the plantations consists either in the sporadic removal of trees (windthrows or selected trees for estate purposes) or by clear felling on maturity. After a longer or shorter interval the ground is replanted. In some, however, the management is far from being intensive, and the natural process of succession has asserted itself.

The account of the vegetation centres round the planted coniferwood, for all other forms are derived from or related to it. The adult wood consists of the tree layer of pine and larch (*Larix decidua*), a discontinuous shrub layer chiefly of rowan (*Sorbus aucuparia*) and a ground flora of dwarf shrubs (*Calluna vulgaris* and *Vaccinium myrtillus*) and wiry grasses (*Deschampsia flexuosa*) dominant. Upon clear felling the conifers the vegetation consists of scattered rowans set in a heath, with *Deschampsia*, *Vaccinium* and *Calluna* sharing the ground. What exactly happens to this community is not known with certainty in all examples, but retrogression to *Calluna* heath can take place. The heath is invaded by subsponaneous pine and gives rise to a pine-heath—this probably being the community nearest to the primeval condition of the vegetation that can be found to-day. If the conifers are selectively removed a rowan-birchwood succeeds the conifer plantation, but it is uncertain how far this rowan-birchwood can maintain itself. Reversion to heath is probable.

Wherever beech grows side by side with either the coniferwood or the rowan-birchwood, invasion takes place and a beech associates finally develops into pure beechwood. These relationships are expressed in the accompanying diagram, but it does not necessarily imply that the beech is unable to invade the communities where such invasion is not shown.



The communities described contain between them twenty-five woody species, seventy-five herbs and grasses and thirty-nine bryophytes—a total of 139. Of the twenty-five woody plants only eleven are certainly native to Aberdeen and adjoining parishes, the rest being planted or subsponaneous<sup>1</sup>. Only the more important species are given in the list (p. 341) where the number of examples in which the species is found and the average frequency are recorded. This list contains eleven woody plants, thirty-two herbs and grasses and seventeen bryophytes. The native woody plants listed are marked N. The fact that only eleven woody species are native indicates to some extent the changes wrought by man. How far some of the introduced plants can maintain themselves has already been answered by Trail in the work cited,

<sup>1</sup> Trail, *Memorial Volume*, 1923.

*Note.* Trail considered that all existing pines are planted or subsponaneous and that none are the lineal descendants of those whose stumps are found in the peat. *Pinus silvestris* var. *scotica* is not recorded from the woods described here.

but the further question of their fate in the absence of man's continued influence is left unsettled.

Among native trees the birches (*Betula* spp.) and rowan (*Sorbus aucuparia*) reproduce successfully in the existing conifer plantations, but the non-native pine apparently cannot do so until reversion to *Calluna*-heath occurs. Thus these pinewoods if left to themselves would fail to maintain their present status, but the pine would continue to exist as a constituent of a pine-heath community.

The introduced trees found in the woods examined are (besides the pine) *Abies lasiocarpa*, *A. pectinata*, *Acer pseudoplatanus*, *Fagus sylvatica*, *Larix decidua*, *Picea excelsa*, *Prunus avium*, *Pseudotsuga taxifolia* (*douglasii*), *Quercus robur* and *Q. sessiliflora*. Seedlings or young plants of *Acer*, *Picea*, *Pseudotsuga* and *Quercus robur* have been seen, but there is no evidence to show that naturally reproduced plants attain maturity. *Abies pectinata* is more successful numerically, but the saplings are mostly killed by *Dreyfusia nüsslini*. Larch regeneration is widespread but not abundant, except locally within the conifer plantations. The most important alien is the beech, whose successful reproduction enables it to compete with the pine, birch and rowan.

The failure of spruce regeneration is interesting. Vegetationally northern Scotland is nearly related to Scandinavia, whose evergreen coniferous forest is dominated by pine and spruce. Absence of spruce from this country in post-glacial times is usually set down to purely historical causes, for, when planted, it grows well, being one of the three conifers commonly used during last century. It also produces fertile seed, yet subspontaneous spruce, although reported from some parts of the country, is not common. The causes of this failure have not been investigated.

The three main species in the ground vegetation are *Deschampsia flexuosa*, *Vaccinium myrtillus* and *Calluna vulgaris*; *Deschampsia* and *Vaccinium* predominate in the woodlands, *Calluna* in gaps and spreading in the felled areas. These are species with a high degree of sociability, in contrast to the majority of their common associates whose inclusion does not materially alter the general appearance. Differences therefore in the physiognomies of the different communities are mainly due to the relative frequencies of these three and to a less extent of those of the other species. The changes are due to various causes, the most obvious being the density of the overhead canopy, but while the new conditions in the beechwoods exclude certain species, none alien to the heath flora is introduced. Other factors influencing the ground vegetation and discussed more fully below (pp. 336-38) are the thickness of the beech litter and tree-root competition.

The full list of bryophytes contains twenty-nine mosses and ten liverworts: many of the latter have only their occurrence noted.

The herbs and bryophytes are those most commonly associated with acid soils, although some with a wider pH range are also found in calcareous soils.

A list of fourteen lichens is added, but the records are incomplete.

The biological spectra of these heathy woods bring out the insignificant place of therophytes and the importance of chamaephytes.

P.	Ch.	H.r.	H.s.	H.c.	G.r.	G.b.	G.rad.	T.	Total
All species (excluding alien phanerophytes):									
13.5 (12)	18 (16)	12 (11)	19 (17)	22 (20)	11 (10)	1 (1)	1 (1)	2 (2)	99.5 (90)
53 (48)					13 (12)				
Ground flora (all species):									
	20.5 (16)	14 (11)	22 (17)	25 (20)	13 (10)	1.5 (1)	1.5 (1)	2.5 (2)	100 (78)
61 (48)					16 (12)				

The spectrum of the ground flora bears on the whole a closer resemblance to the *Deschampsia* than to the *Holcus* type of shelterbelt beechwoods (Part I, p. 149). Here, however, although the difference is small, the caespitose hemi-cryptophytes show the highest percentage.

Perhaps the most impressive feature of the woodlands is the evergreen carpet of ground vegetation due primarily to *Deschampsia* and *Vaccinium* but enhanced by the bryophytes and many winter-green vascular plants. There is no spring facies such as is produced by *Anemone nemorosa* in Type 1 woodlands, and the species with showy flowers are few—*Oxalis acetosella*, *Potentilla erecta* and *Trientalis europaea* being the most important.

#### SOME FACTORS INFLUENCING THE COMPETITION BETWEEN PLANTS.

##### (1) *Soil depth, root systems and height growths of trees.*

The gale on January 27th, 1927, exposed the root systems of many trees. Some of these were examined but not enough to warrant generalisation respecting the structure of the root system of the different species. Indeed the impression was gained that in some the structure was an expression of soil environment rather than of inherent tendencies. Two general features stand out. First, the bulk of the root system is confined to the weathered part of the soil, being prevented from deeper penetration by the pan or in its absence by the compact parent soil material. Where the pan is well developed and continuous the under side of the root system is moulded to it and rarely do isolated roots penetrate a few inches below. Indeed the roots sometimes adhere so firmly that in a blown down tree the line of rupture between the root system and the soil lies just under the pan. Where there is no pan the under side of the root system is less even, but is on the whole flat, with a varying number of vertical roots—often in rows—penetrating crevices in the un-weathered soil. The second general feature is the concentration of numerous important roots in the superficial soil layers. These radiate outwards and run on or near the surface of the mineral soil. This is regarded as an indication of a badly ventilated soil, and indeed, in poorer parts of young pine plantations the roots are almost limited to this zone.

The root systems conform to three general types (Fig. 5): (1) in which the roots apart from the superficial ones are generally diffused through the soil (beech, spruce, pine, larch and silver fir); (2) in which the roots are con-

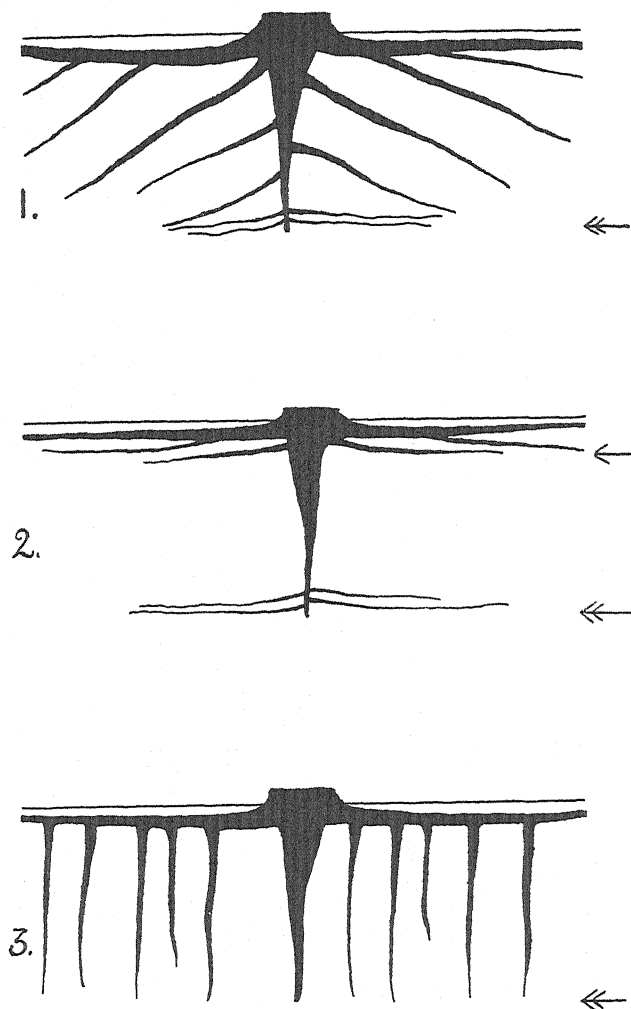


FIG. 5. Diagrammatic representation of three types of tree root systems in podsol: (1) diffuse, (2) layered, (3) sinker. The main roots are superficial in all three types and run just in the grey layer or partly in the grey layer and partly in the raw humus above. ← indicates the level of the compact boulder till or iron pan lying on it; ← the level of the soft humus iron pan in the coffee-brown horizon.

centrated in two horizontally extending layers, an upper supplementing the superficial roots and extending down to the first pan and a lower spreading above the second pan (silver fir); and (3) a superficial root system with vertical sinkers (pine and silver fir). From these observations the impression is gained

that silver fir is more easily discouraged by obstacles than the other trees examined and its root structure appears to be a closer expression of soil environment than that of the other trees.

The inability of deep-rooting trees to produce a root system normal for the species will set a limit to their power to compete with shallow rooters and with trees whose root systems may be described as accommodating. If the rate of growth and the height attained at maturity are regarded as a measure of the power of the environment to satisfy the needs of the species then the following data for five species show that silver fir and beech have a decided advantage over larch, spruce and pine. Their competitive ability is further enhanced by the fact that the former are tolerant, while larch and pine are intolerant of shade. While our knowledge of the influence of the several habitat factors on the growth of these five species is not complete, it may not unreasonably be concluded that these shallow heath soils are limiting the growth of pine and larch.

*Height growth of trees.*

Species	Number of trees measured	Average height	Approx. age
<i>Abies pectinata</i>	4	81 ft. 6 in. (75.5-90 ft.) 24.8 m. (23-27 m.)	—
<i>Fagus sylvatica</i>	22	71 ft. 4 in. (63-80 ft.) 21.8 m. (19.2-24.4 m.)	—
<i>Picea excelsa</i>	12	65 ft. 6 in. (20 m.)	104
<i>Larix decidua</i>	32	65 ft. (19.8 m.)	104
<i>Pinus silvestris</i>	28	60 ft. (18.3 m.)	104

That beech has an accommodating root system is well established from numerous observations in this country: the same cannot be said for silver fir. Indeed continental authorities classify the fir among deep rooters, but in the neighbourhood of Aberdeen, silver fir stands head and shoulders above other conifers, and in view of the data given, it is classified along with the beech. It is therefore considered that the accommodating root systems of beech and silver fir are important factors in enabling these trees to attain the heights they do. The relatively high content of the soil in minerals probably contributes to this result, for the total need of silver fir and beech is higher than that of larch and pine and the supply available does not discriminate in favour of the less exacting. Nevertheless the failure of silver fir (and spruce) to reproduce successfully removes both from the list of beech competitors in the plant succession.

(2) *Light requirements of important species.*

Arranged in descending order of their light needs the important trees in the succession are: birch, larch, pine, rowan, beech. Thus beech can compete successfully with and ultimately replace pine and larch of the conifer plantation



and also birch and rowan of the rowan-birch associates. Rowan occupies a peculiar position. Seedlings and young plants can withstand the heavy shade of beech and normally it forms a shrub layer to trees of taller growth, but it shares dominance with the birch in the rowan-birch associates.

The three most important subsidiary species—*Deschampsia flexuosa*, *Vaccinium myrtillus* and *Calluna*—form an ascending series of light requirement. *Deschampsia*, while it thrives and flowers abundantly in full light can yet endure a very low light intensity, but under canopy shows markedly reduced vigour and flowering. *Vaccinium* with a higher light minimum finds its optimum for vegetative growth in open woodlands and does not respond to additional light except by more frequent flower and fruit production. *Calluna*, on the other hand, has a high light requirement and flourishes only in open conditions. Thus these three become dominant successively as the conifer wood opens out, and mark distinct stages in the life history of the even-aged planted wood.

It may be noted here that while increasing shade kills *Calluna* outright, *Vaccinium* shows greater adaptability by pushing out young shoots from the rhizomes of the killed-back tall stems, and may maintain itself as a small plant under conditions determining the dominance of *Deschampsia*.

### (3) *Tree root competition and the subsidiary vegetation.*

That light is not the sole factor determining the composition and condition of the subsidiary vegetation of woodlands was clearly shown by Fricke (5). He considered that on poor sandy soils lack of water, due to tree-root competition, prevents the growth of herbs and grasses even where the light intensity is above the minimum for these species. To test this conclusion for beechwood an experiment was laid down in a shelterbelt whose ground vegetation consisted mainly of a patchy growth of low-growing and pale green *Deschampsia flexuosa*. Flowering stems were scarce. An area  $3 \times 6$  ft. ( $0.9 \times 1.8$  m.) was selected between and equidistant from two beech trees and surrounded by a trench 18 in. (45 cm.) deep. *Deschampsia* was present naturally inside and outside the plot. At the same time two rows of *Holcus mollis* were planted extending across the plot on to the ground outside, and a control plot comparable in position to the "trenched" plot was similarly planted with *Holcus mollis*. Subsequently smaller plots were laid out in a number of woods: four in shelterbelt *Deschampsia* beechwoods, two in pine-woods, one in a rowan thicket, and one in a rowan-birchwood. All these were laid out so as to obtain some idea of what to expect and note more carefully in contemplated detailed and critical experiments, which circumstances prevented.

From these preliminary experiments the following general observations were made on the vegetation inside the plots:

- (i) In all the plots except the two last mentioned (rowan and rowan-birch)

there was a distinct increase in vegetative vigour shown by *Deschampsia flexuosa*, *Holcus mollis*, *Luzula pilosa* and *Oxalis acetosella*. There was no change in the vigour of *Vaccinium myrtillus*.

(ii) *Deschampsia* and *Holcus* were distinctly darker green.

(iii) *Deschampsia* and *Oxalis* began growth, or at least grew much more vigorously, earlier in the year. *Oxalis* flowered earlier.

(iv) The flowering stems of *Deschampsia* and *Holcus* were more numerous.

(v) In the rowan thicket there was no noticeable change in the *Deschampsia*. Here the *Deschampsia* was initially much more vigorous.

(vi) In the rowan-birchwood it is doubtful if there was any difference.

(vii) In one plot with bare patches of soil the flora was richer inside than outside, and while no definite record of the floras was made at the time of establishment of the experiment and consequently no certain conclusions can be drawn, yet it is believed that the vegetation increased since the laying down of the plot. Older abandoned plots, instituted for another purpose, also bear a richer flora.

The behaviour of *Vaccinium myrtillus* is outstanding: it is not affected by tree-root competition. To test this further a sod (approx.  $10 \times 20 \times 7.5$  cm. deep) of *Vaccinium* with stems 7.5–10 cm. high was set into a trenched plot under dense beech where the *Deschampsia* was low growing and patchy and where no *Vaccinium* was present naturally. At the same time another sod of the same size was set into the ground outside the plot. In this case of course the roots were cut at a depth of 7.5 cm., but the lapse of time would allow the roots to invade the sod, whereas in the "trenched" plot the roots were cut annually. The response was the same in both cases. The original stems died back and new slender shoots with small leaves took their place. At the end of 30 months (covering three vegetative seasons) the average height of nine *Vaccinium* shoots from inside the plot was 2.1 cm., of twelve shoots outside 1.93 cm. From the experimental evidence, then, tree-root competition does not affect the condition of *Vaccinium*, and it is highly probable that light is the limiting factor. Even in this situation where *Vaccinium* is a small, much attenuated plant, *Deschampsia* responds to the cutting of the tree roots by increased vigour, by becoming darker green and by producing flowers.

#### (4) Depth of leaf litter.

The composition and condition of the ground flora are also influenced by the leaf litter which may in places be sufficiently bulky to cover up and kill out plants of low-growing habit. The low-growing habit may be induced by conditions such as light and root competition. For example, the exposed floor of shelterbelts from which the litter is blown away may be dominated by low-growing *Deschampsia*, but if a layer of beech leaves 5 cm. thick is laid down and held in position by wire netting then the *Deschampsia* is killed out, and this result cannot be due to any toxic substance produced by the dead

leaves because where occasionally *Deschampsia* leaves project above the surface they not only survive but attain greater luxuriance than without the litter. The lethal effect may be due merely to cutting off the light. On the other hand *Holcus mollis* is much improved by similar treatment, as shown in its increased vigour, darker green colour and the production of flowering stems—a result essentially similar to that brought about by cutting the tree roots. And wherever species of stiff erect form such as *Holcus* and *Vaccinium* stay the flight of leaves which thereby accumulate between the stems, then plants like liverworts, mosses, low-growing *Deschampsia*, *Galium saxatile* are buried and killed. The remains of *Deschampsia* found below is evidence of this process. The absence of a *Deschampsia* mat in sheltered beechwoods, where the litter is derived from the normal fall of leaves is thus explained. Occasionally *Deschampsia* is found, but always on boulders, tree stumps or little knolls projecting above the general level of the soil surface.

#### (5) *Conditions for germination and establishment.*

Again difficulties connected with germination and establishment may account for the absence or much reduced frequency of plants from places where they would be expected. Open conifer woodlands sometimes show *Deschampsia* forming a mat when the light intensity is clearly adequate for *Calluna vulgaris*: for when the turf is removed the ground is readily colonised by *Calluna*. It is not suggested that the *Deschampsia* mat could hold out indefinitely against *Calluna* (p. 343), but it is clear that between the time when light conditions become suitable and the actual response in succession there may be a considerable lag, so that the absence of plants from an area at any one time is not immediately interpretable in terms of the existing physical factors.

These observations throw light upon the dominance of *Deschampsia* in exposed shelterbelts and its replacement by *Holcus* where the leaf litter lies, also on the distribution of *Holcus* in the *Deschampsia* woods (Part I, p. 148).

It may be concluded then that light is a factor influencing the composition of the subsidiary vegetation, but that the absence of a plant does not imply that the light intensity is below the minimum for that species: that tree-root competition is a factor influencing both the composition and condition of the vegetation, but that it is without influence upon *Vaccinium*: that light and tree-root competition may so influence the condition of the vegetation that they allow leaf litter to exercise an influence upon its composition: and that leaf litter may also influence the condition of certain plants.

#### (6) *Biotic factors.*

The paramount influence of man has been noted already. Among animals, rabbits are the most important. They are present in relatively small numbers due perhaps to the unsuitability of the soil for making burrows, aided by systematic shooting on Countesswells and by disturbance at Hazelhead. At

Fintray, however, rabbits are more numerous, and locally they keep down rowans and birches in an area cleared of timber. So far as observations go rabbits cannot be considered to have a permanently stabilising influence on the subsidiary vegetation, although they may alter the rate of change. It may, however, be recorded that *Deschampsia flexuosa* is cropped close where artificial nitrogenous manures have been added to the soil. Otherwise *Deschampsia* is not noticeably affected by grazing, nor is *Calluna*. Rabbits (with hares) do considerable damage to newly planted conifers.

The effect of animals upon trees has not been the subject of investigation, and in the absence of experimental data it is unsafe to assume that the known effect of the biotic factor on beech regeneration applies in equal degree to other trees. The supply of seed is, however, considerably reduced by the activities of squirrels, which eat the seeds of pine, larch, spruce, douglas fir and beech.

#### THE PLANTED CONIFERWOODS.

Four of the seven woods examined are mature: the other three are younger but old enough to have initiated the essential structure of mature woods. This consists of a tree layer of planted conifers, a shrub layer of rowan, and a subsidiary vegetation of dwarf heathy shrubs, grasses, herbs and mosses commonly found on acid soils.

*Tree layer.* It was a common practice of foresters to plant a mixture of pine, larch and spruce. Some of the woods investigated are probably the results of such planting, for the three species are found in all except in one which has no larch. But whatever the original proportions the dominant tree is now the pine, with, in one wood, larch dominant and pine frequent. The spruce is generally an occasional to locally frequent constituent, and silver fir is local.

Although the pine is severely attacked by squirrels, whose peeling of the bark leads to the formation of a bushy crown, it looks the most healthy of the trees. Larch suffers badly from canker, two or more leading shoots generally replacing the original leader, and both pine and larch show much heart rot (*Fomes annosus*). Of the broad-leaved trees beech is the only one to attain dimensions at least equal to the conifers. Birches<sup>1</sup> are frequent and may reach a height of 58 ft. (17·7 m.). An occasional *Quercus robur* is met with in two woods and one tree reaches 35 ft. (10·7 m.). No acorns are produced and Trail does not consider oak native to the immediate neighbourhood of Aberdeen.

In regeneration the most successful trees are birch and beech, both being represented by trees of varying size from seedlings upwards. Of the conifers larch gives some show of natural regeneration and all ages are found: the pine,

<sup>1</sup> In addition to *B. alba* and *B. pubescens*, there are many "intermediate" forms. A systematic study of the numerous forms of birch in the North of Scotland is needed.

on the other hand, fails, no young growth having been observed although seedlings were collected in one wood. Occasional young spruces are found and they may be subspontaneous, whilst the few young silver firs are generally in a dying condition.

*Shrub layer.* The shrub layer of rowan is of uneven density. Poorly represented in some parts, even where the light intensity is adequate, it forms thickets in others—generally under opener canopy. Whilst the cause of this variation is unknown it is correlated with the growth of the pine, for in young pole woods where the pines grow faster the rowan is much more common (p. 342). Rowans of all ages are found, but many of the small ones occurring under dense canopy are several years old. Many are grazed by rabbits.

Other constituents of the shrub layer are *Ilex aquifolium* (o.), *Lonicera periclymenum* (l.), *Sorbus aria* (o.), whilst *Rubus fruticosus* (agg.) and *Rubus idaeus* are mostly local.

*Ground flora.* Fifty vascular plants and twenty-nine bryophytes are recorded.

	No. of examples in which species occur						
	7	6	5	4	3	2	1
Vascular plants	11	5	3	2	2	9	18
Bryophytes	10	4	0	2	3	4	6

Their distribution in the examples shows the relatively high numbers found in all, whilst one-third of the vascular plants and half of the bryophytes occur in six or seven of the woods. This high constancy is combined with a relatively high average frequency, all species except *Blechnum spicant*, *Holcus lanatus*, *Rumex acetosella*, *Thuidium tamariscinum* and *Dicranella heteromalla* having values of 2.0 or over (list of spp. p. 341). The frequency of *Calypogeia trichomanis*, which comes into this group, is not recorded.

*Deschampsia flexuosa* is the most frequent plant, covering the ground with a low-growing carpet where the pines are denser, but under opener canopy sometimes forming a thick mat. Flowering is fairly common although not abundant, but after carting and haulage of stems *Deschampsia* flowers profusely between the cart tracks, the trail standing out conspicuously from the surrounding vegetation.

For reasons already given the condition of *Vaccinium* is probably a truer index of the light intensity reaching the floor of the wood. Where *Deschampsia* forms a low mat *Vaccinium* is small (7.5–10 cm.) and although occasional to frequent it is inconspicuous; but with the opening up of the wood it assumes dominance, supporting the long straggling leaves of *Deschampsia* and attaining an average height of about 25 cm. Locally it may reach 75 cm.

*Calluna* is sparsely distributed through the woods but becomes abundant only in open gaps: and this succession to *Calluna* in gaps has not always taken place. This may be due to purely biological causes, for although *Calluna* may be found under a continuous pine canopy as a small attenuated plant 7.5 cm.





high, yet it is not common, and colonisation by seedlings of a mat of *Deschampsia* probably presents great difficulties. On the other hand there is some evidence to show that in these heathwoods dominance of *Calluna* sometimes indicates local soil change.

Although present in all the woods the distribution of *Oxalis acetosella* within them is irregular. Patches with *Deschampsia* and *Vaccinium* dominant may be found with or without *Oxalis*. *Oxalis* is occasionally found growing through clumps of *Sphagnum*.

Emphasis has already been laid on the combined action of certain factors in causing local variation in the ground flora. Wherever a deep shade is cast, for example by thickly foliated trees like beech and spruce, by a double canopy of pine and rowan, or of rowan and *Lastrea dilatata*, there the weakened light intensity, aided by root competition and leaf litter, excludes or almost excludes *Deschampsia*, and *Oxalis*, *Trientalis* and small *Vaccinium* become the prevailing plants. In the neighbourhood of beech, bare soil is occupied by dominant *Deschampsia*, where the litter is 2.5 cm. thick, *Deschampsia*, *Oxalis* and *Vaccinium* are found, and where over 2.5 cm. only *Oxalis* and *Vaccinium*.

An analysis of the raw humus layer shows that recent *Deschampsia* and *Vaccinium* humus overlies a layer of black peat: on the other hand below *Calluna* and *Vaccinium* humus is found a layer of *Deschampsia* remains.

From these data the major changes in the vegetation during the later stages in the life history of the conifer plantations can be made out. A two-layered community of trees and *Deschampsia* is first identified. At this stage rowan comes in but remains small except under opener canopy. This is succeeded by a three-layered community consisting of (1) trees, (2) a shrub layer of rowan, and (3) *Vaccinium* dominant in the ground flora. Finally *Vaccinium* gives way to *Calluna*, only in quite open gaps.

The ground, however, is not uniform, and preliminary observations in younger conifer plantations reveal differences which are obscured in the adult woods. For example in a young pinewood about 17 years old and planted on ground which formerly carried a conifer crop, the height and density of the trees vary much from place to place. Where the trees are taller and dense the ground is carpeted with needles, the removal of which reveals a thick layer of dead *Deschampsia*. Where the trees are shorter and less dense, luxuriant *Calluna* dominates. Again in a wood 33 years old there were three quite distinct facies, respectively correlated with the different height growths of the pines. In these the dominant plants are *Oxalis*, *Deschampsia* and *Calluna*, and the average height of the pines was 44.8 ft. (13.7 m.), 36.7 ft. (11.2 m.) and 22.5 ft. (6.9 m.). The average number of rowans in 10,000 sq. ft. of the three types was 26.8, 6.4 and 4.0.

With the data at present available it is premature to make further comparison and deduction, but three distinct seres, separable by the vegetational changes taking place during the life history of the woods, are suggested.

## FELLED AREAS.

Near to and in some examples adjoining the woods just described are five areas on which the adult planted conifers have been clear felled. Although cut at different dates—one before 1914, three during 1914–19, and one during the winter 1923–4—the vegetation of the felled area still bears the impress of the conifer canopy and the uncut self-sown beech, larch, birch and rowan of varying age are set in a patchwork of *Deschampsia*, *Vaccinium* and *Calluna*—their distribution reflecting, less faithfully with the passing of time, the density of the overhead canopy.

Apart from new species of sporadic occurrence there are none which can be picked out as tending to change the aspect of the vegetation. Change does not come by the replacement of the existing vegetation by new species but by the elimination of woodland species and an alteration in the proportions of those already present. Of the woodland species *Oxalis* lingers in shaded places, for example under isolated beeches, clumps of birch and rowan and in the hollow of a decaying stump. It is decidedly more frequent in the recently cut wood but rare (occurring only in a hole in the ground) in the area felled before 1914. *Lastrea dilatata* is suffering the same fate and surviving individuals are smaller and paler in colour than under canopy. *Goodyera repens* goes out soon after felling.

The altered conditions affect the bryophytes to a greater extent. *Calyptogeia trichomanis*, *Dicranella heteromalla*, *Hylocomium loreum*, *Hypnum cristacastrensis*, *Mnium hornum* and *Thuidium tamariscinum* are almost or quite eliminated, whilst the following show a decidedly reduced frequency: *Hylocomium triquetrum*, *Lophocolea bidentata* and *Plagiothecium undulatum*. On the contrary *Hypnum cupressiforme* and *H. schreberi* show an increase.

After the felling of the trees and exposure to full sunlight *Deschampsia* is stimulated to vigorous vegetative growth and profuse flowering, and it rapidly forms a thick mat of raw humus. *Calluna* responds in the same way but *Vaccinium* shows no noticeable change, although it flowers and fruits more abundantly than in open woodland; only those suppressed individuals found under the heavier shade in the woodlands increase in size, but show little sign of spreading. The altered conditions therefore favour *Deschampsia* and *Calluna* relatively to *Vaccinium*. When comparison is made between recently and older-felled areas the persistence of the patchwork is noticeable, each of the three species holding its own with remarkable tenacity. The final struggle lies between *Deschampsia* and *Calluna*: and *Calluna* wins. The following evidence supports this. The patches of heather are extending vegetatively at the expense of *Deschampsia*, the dead remains of which are found under the advancing margin. But the mat of *Deschampsia* is unsuitable for *Calluna* ecesis, and seedlings are found only near and on stumps, along rabbit runs, and on old cart tracks. Further, a fringe of *Calluna* is commonly found bordering

footpaths. Thus while *Deschampsia* offers formidable barriers to *Calluna* establishment, which are locally broken down by biotic influences, yet the ultimate—though delayed—dominance of *Calluna* is assured and the felled area passes over to heath. The heather owes its supremacy to its taller and denser growth form, particularly when young. As it grows older it becomes “leggy,” opener, unable to remain upright and allows a luxuriant growth of mosses.

The trees left behind after felling must have found suitable conditions for germination, establishment and growth in the planted coniferwood. The question now arises how far these are capable of multiplication in the changed conditions. There are, it is true, many individuals of rowan and birch which look as if they are quite young and had sprung up after felling, but these may be, and very probably are, the suppressed individuals which are found in the denser parts of the adult wood and which have responded to the increased light intensity. No small rowans and birches can definitely be said to have germinated and grown up after felling, and it appears as if the mat of *Deschampsia* is unsuitable to their establishment. An experiment laid down to test this as yet yields no results, but the frequency of rowan and birch bears no relation to the duration of the period since the wood was felled. In the absence of experimental proof it is premature to give a decisive answer, but the belief is held that, even if some rowans and birches do appear, the rowan-birchwood to be described later does not arise *de novo* by the invasion of felled areas<sup>1</sup>.

On the other hand when reversion to heath takes place, pine is clearly the most successful, although it is never an abundant, invader, whilst scattered birch and rowan are also found. But the available evidence goes to show that *Calluna* remains dominant and that pine, birch and rowan exist as isolated trees unable to reconvert the heath to woodland. Beech is occasionally found as a survivor from woodland, but old trees, grown for more than a century on the edge of “natural” undrained heath, are unable to colonise it (Fig. 3).

#### THE ROWAN-BIRCH ASSOCIES.

We have just seen that the clear felling of conifer plantations does not give rise to conditions suitable for free colonisation by rowan and birch. Yet undoubtedly the rowan-birch associates occupies the site of coniferous woodland, and the question arises under what conditions can a coniferwood be followed by a rowan-birchwood and thereby hindered from retrogressing to heath? Evidence on this question has been obtained from four areas—three of them narrow strips to leeward of beechwoods (Fig. 3, and Fig. 1, Part I), and one occupying several acres and a relatively isolated position on a north-facing slope (Fig. 1). The description given applies mainly to this last. None of the woodlands has reached maturity.

<sup>1</sup> An enclosure was made in the summer of 1928 and was last examined in September 1930. No seedlings of birch or rowan had appeared. The most significant change was the spread of *Calluna* at the expense of *Vaccinium* and *Deschampsia*.

Rowan and birch are present in varying proportion, with rowan generally more abundant than birch, but each may be locally dominant. The average height of the birch is from 20–25 ft. (6.1–7.4 m.), rowan 16 ft. (4.9 m.). Whitebeam is an occasional constituent. Beech (o.—ld.) of all ages (from seedlings upwards) and forms (from pioneers with widespreading crowns to poles free of lower branches) is found, and it is clear that this species is spreading, though slowly. One older beech is 60 ft. (18.3 m.), and thus far outstrips the rowan and birch. Conifers are generally occasional but may be locally dominant in small groups of planted and relatively young trees. Subspontaneous larch and spruce are local, and occasional young pines of varying age are found. Conifer stumps are found throughout the wood, many being buried by the growth of *Vaccinium*.

A comparison of the ground vegetation of coniferwood, felled area and rowan-birchwood reveals what exactly has happened. This comparison (list of spp. p. 341) shows that on the whole there is general agreement between the frequencies in the two woodland communities and that the values found in the coniferwood and altered (either up or down) by felling, tend to be reproduced in the rowan-birchwood. But there are certain anomalies: *Calluna* maintains its increased frequency, *Deschampsia* shows a significant drop, and *Vaccinium* a big increase. Some account of these species and one or two others is given before an explanation is offered.

By the formation of a canopy of birch and rowan a change in the relative frequency of the three main species has recently taken place—the change being the reverse of the succession of stages found in the growing coniferwood. *Vaccinium*, which averages 25–37.5 cm. under a varying but open canopy, in open places reaching 90 cm., is replaced under shade by a carpet of *Deschampsia* in which *Vaccinium* shoots 7.5–10 cm. high rise from the rhizomes of the taller and still erect but dead shoots. The discontinuous patches of *Calluna*—as distinct from the gaps where *Calluna* is dominant—give way directly to *Deschampsia* without showing an intermediate stage of *Vaccinium*. Thus *Vaccinium* has been more abundant than it is now, and *Deschampsia* is spreading at the expense both of *Calluna* and *Vaccinium*. This result is probably due mainly to the increase in size of the individual trees and not so much to their recent increase in number.

Among other species of which mention may be made *Goodyera* is rare and *Lastrea* shows a reduced frequency compared with that in the adult coniferwood. *Oxalis* is generally frequent and is found among *Vaccinium* and *Calluna* except where the latter is dominant. Local soil variation is perhaps indicated by the greater frequency of *Oxalis* where birch is locally dominant. Here the humus is less raw and this local variation perhaps corresponds to the young coniferwood with *Oxalis* dominant (p. 342).

An interpretation of these phenomena is now advanced. From the occurrence even in open places of the essential constitution of a woodland flora it

is clear that the areas never retrogressed to heath: but it is equally clear that the conditions allowed *Calluna* and especially *Vaccinium* to spread. Now *Vaccinium* does not show extension in the felled areas, and the conclusion reached is that both *Vaccinium* and *Calluna* spread under conditions such as those which obtain in an open coniferous woodland. This is supported by the evidence from the occurrence of *Deschampsia*. Although spreading, this species shows a reduced frequency compared with that for the adult coniferwood taken as a whole and the felled area, a frequency such as is found in those parts of coniferous woodland which are dominated by *Vaccinium*. Again, the general distribution of *Oxalis* even in places where the wood is open indicates that full exposure has never been so great nor so prolonged as to eliminate *Oxalis* from the flora, as happens after felling of the conifer plantation. The reduction in frequency of *Oxalis* in opener areas bearing *Vaccinium* is paralleled by the similar reduction in the later life history of the coniferwood when *Vaccinium* becomes dominant.

A coniferwood which was gradually opened out either by wind throws, as is evidenced locally from the upturned roots, or by selective felling, would provide the conditions found suitable for the extension both of *Calluna* and *Vaccinium*, and the preservation of shade plants like *Oxalis*. The openings made were colonised by birch and rowan, which, growing up in thickets, suppress *Vaccinium* and *Calluna* and enable *Deschampsia* once more to spread. Thus the rowan-birch associates may be considered the lineal descendant of the shrub layer of the planted coniferwood.

In one area (Fig. 1) a fragment of the rowan-birch associates Type 1, exists. The birch is taller (35-40 ft.: 10.7-12.2 m.) with rowan forming a shrub layer reaching to 20 ft. (6.1 m.). Young beech is occasional, and the pole beeches have the clean-looking white stems characteristic of thriving trees. In the subsidiary vegetation *Calluna* is occasional, *Vaccinium* abundant to dominant, *Deschampsia* and *Oxalis* frequent to locally abundant and *Pteridium* locally dominant, reaching to 6 ft. (1.8 m.). The most noteworthy difference is found in the abundant *Anemone* which is occasional or local only in the other type.

As to the fate of the rowan-birch associates nothing definite can be said, but a doubt may be expressed of its ability to maintain itself indefinitely. As the trees grow older and open out *Calluna* will spread from those nuclei where it is definitely established and in which subspontaneous pine appears as the most successful invader. Thus in the diagram on p. 331, although this retrogression is marked doubtful it is regarded as likely to occur. From observations in other areas on Deeside, its existence in Type 1 as a self-reproducing unit, is scarcely in doubt.

#### THE BEECH ASSOCIATES.

The beech associates has its origin in the invasion by the beech of the adult coniferwood (Fig. 7 and list of spp. p. 341, column 2) or the rowan-birchwood

(Fig. 6 and column 5). The lists of species, obtained from three and four examples respectively of the two associates, which are of different origin, are given separately, although it appears certain from the size of a few of the beeches that beech existed in the coniferwood which preceded the rowan-birchwood and that some regeneration took place before the conifers were removed. No separate treatment is therefore given.

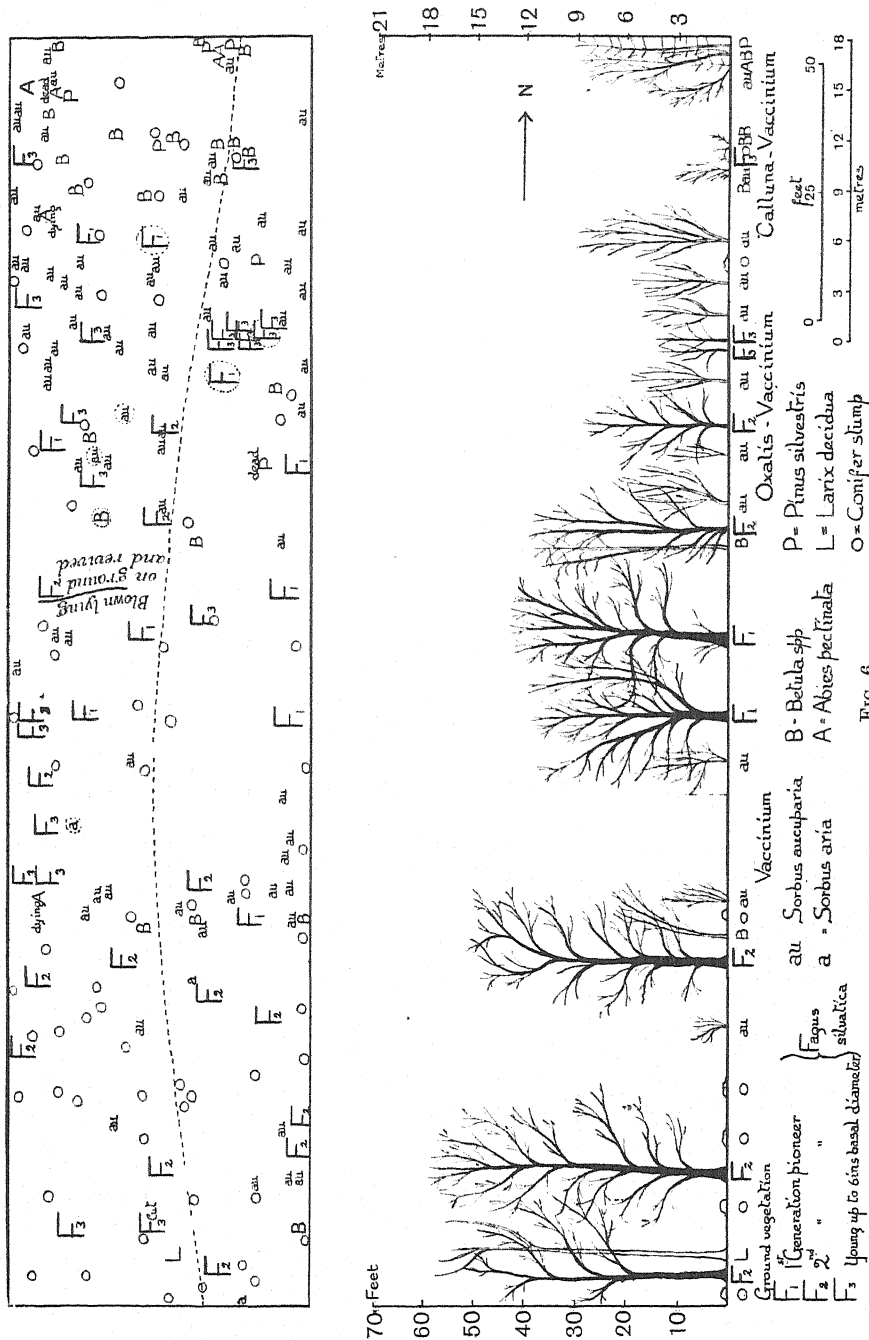
In all examples it is clear that the origin of the invading beech is from the shelterbelt beechwoods adjoining (Figs. 1, 2, 3, and Fig. 1, Part I) or from marginal trees aided by an occasional old beech in the invaded woodlands (Fig. 3). The width of the invaded zone is in all cases small, an observation which supports conclusions already reached on the slow rate of beech migration.

The frequency of the beech varies much in the different examples and in different parts of one and the same woodland. Generally abundant, it varies from occasional to dominant. The frequencies of the other trees vary similarly, with rowan the most frequent in the rowan-birch-beech associates (average frequency 4.3). Dead birch, rowan and whitebeam—the two last surviving longer and sprouting from the base when the main stem is killed by shade—bear witness to the advance of the beech.

The age of the beeches ranges from seedlings to fairly old trees. Some examples show a fairly uniform number of stems of different ages: in others there is a high proportion of one age, mostly large saplings (contrast Figs. 6 and 7). The one extreme shows the method of invasion called "enclave" invasion already described in my account (28) of the beech's entry into and conquest of the narrow ash-oak associates of the South Downs; the other, mass invasion by the progeny of a good mast year under conditions suitable to the survival and growth of the young plants. The forms of the stems and crowns vary according to the method of invasion and the density and height of the accompanying trees. Thus mass invasion with or without the overhead canopy induces the formation of fairly straight stems, but pioneer forms appear under open conditions and are therefore found only in the associates derived from the opener parts of rowan-birchwood.

The most notable change in the ground vegetation is the reduction in number and frequency of vascular plants, from fifty in the adult pinewood to twelve in the beech associates derived from it, and from fifty-one in the rowan-birch associates to twenty-two in the corresponding beech associates. This reduction, due to the entry of the beech, is brought about by the density of the overhead canopy, by root competition and by the thickness of the beech leaf litter, the normal leaf fall in many examples being augmented by the litter blown from the shelterbelt beechwoods on the windward side. Influenced by these factors acting separately or together the frequency of the different species varies in the different examples and in different parts of the same example: parts of the floor are almost devoid of plants, parts bear relict vegetation of the invaded woods.





The diminution in the light intensity, most marked where the beech forms a continuous under-canopy to conifers, eliminates or causes a reduction in the frequency of light-loving plants such as *Calluna*, which survives in gaps only. The behaviour of *Vaccinium* reflects the change that has taken place. Dominant in gaps, sometimes reaching 75 cm., its stems are killed back under heavier shade but are replaced by new shoots (10–15 cm.) coming up from the rhizome. Its former abundance is demonstrated by removing the beech litter, under which there is found a layer of rhizomic remains. *Deschampsia*, as a small plant, survives the heavy shade on boulders or small mounds where the leaf litter does not lie. Locally under the leaf litter its dead remains are found.

While the presence of leaf litter thus aids in reducing the number and frequency of species, handicapped by root competition and shade, it brings into prominence those which can accommodate themselves to it or are actually favoured by it. Thus in parts of the conifer-beech associates, where the shade is not limiting, the frequency and vigour of *Oxalis* is increased. From measurements of the length of the petioles *Oxalis* can survive in beech leaf litter to a depth about 15 cm., and wherever the plant is found growing in litter apparently exceeding this depth, investigation shows it to be rooted in the humus capping a boulder projecting above the surface of the mineral soil. *Trientalis* also survives in 15 cm. of leaf litter, but where the litter is of greater depth *Lastrea* and *Vaccinium* are the sole survivors—the former under shade, the latter in gaps.

In the conifer-beech associates there are only fifteen bryophytes as compared with twenty-nine in the adult conifer wood, but there is a reduction of three only (from twenty-six to twenty-three) in the rowan-birch-beech associates. The explanation of the difference probably lies in the less complete occupation of the ground by the beech and the provision, on the upturned conifer root systems, of mineral soil uncovered by leaf litter. On the whole there is a reduction in frequency similar to that found for the vascular plants, and locally the survival among the beech leaf litter of the taller-growing species of *Polytrichum*, of *Dicranum scoparium* and *Hylocomium triquetrum* is noticeable.

The beech associates of Type 1 is represented by two woodlands, one occupying the south slope of Fintray Wood (Fig. 1). The other is not figured but is found on the Countesswells Estate about half a mile west of the woodlands depicted in Fig. 2. The former is derived from the rowan-birch associates, which, as the stumps show, was in turn preceded by a conifer wood; while the latter

Fig. 6. Ground and profile transect (along the line *CD* in Fig. 3) from near the edge of the planted beechwood (to the left, beyond the figure) through the beech-rowan-birch associates and the rowan-birch associates. The direction of beech invasion is from left to right. The site was originally occupied by a coniferwood (v. stumps). This had already included some beeches (large *F*<sub>1</sub> and *F*<sub>2</sub>). To the right of the figures the ground is colonised by *Sorbus aucuparia* and some *Betula* forming the rowan-birch associates. This is now being invaded by beech. The profile transect includes trees in the neighbourhood of the broken line and shows the stem and crown forms and the relation of the beech to the other trees.

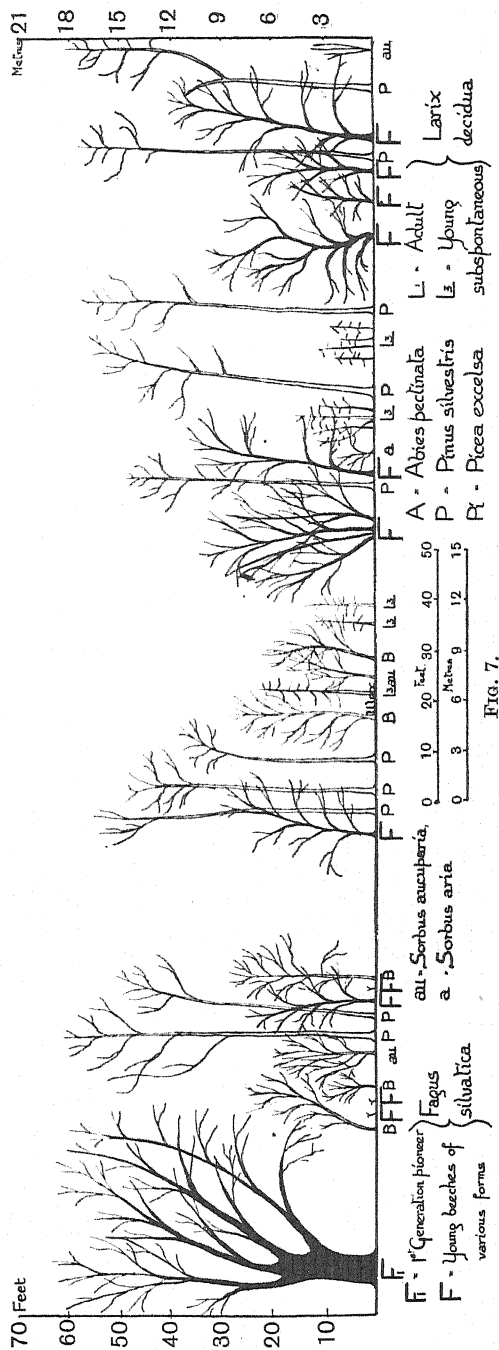
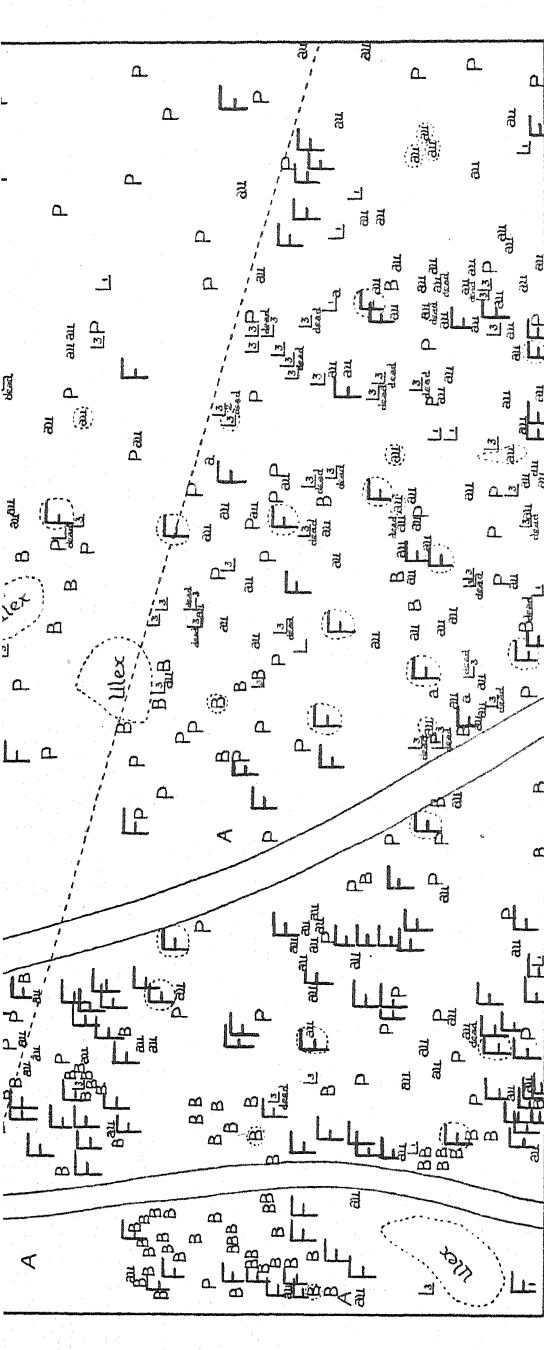


FIG. 7.

originates by the invasion of a coniferwood from marginal and old beeches within the wood and coeval with the conifers. These woodlands show a structure similar to that described and both enclave and mass invasion are represented. The older beeches are on the whole taller and the saplings and young poles are straighter and with whiter bark than in the woods already described.

Here *Vaccinium* is much less conspicuous and instead of a layer of rhizomes under the leaf litter there is found a structureless peat, indicating a more rapid decomposition of the raw humus. But dead erect stems are found and a layer of rhizomes caps projecting boulders. The chief difference, however, lies in the spring facies of abundant to dominant *Anemone*. *Oxalis* is occasional to co-dominant.

Part of the Fintray Wood (Fig. 1) is exposed to southerly winds. The dominance of the beech is more complete, a shrub layer is absent and the wind blows freely below the canopy (height of beech up to 74 ft. or 22.5 m.), leaving in the foreground a rubble of beech cupules and in the rear a compact stratum of laminated beech humus which had accumulated when the associates was younger and the sphere of action of the wind less extensive. Under this layer of humus are found the remains of *Vaccinium* with some *Deschampsia*.

The ground is almost devoid of plants. *Vaccinium* to 5 cm. is occasional: *Deschampsia* is occasional but locally dominant on the southern margin where there is more light. *Anemone* is occasional, small (2.5 cm.) with small leaves and not flowering. *Pteridium* is occasional (up to 30 cm.) under shade, and locally dominant along the margins. *Oxalis* is not recorded.

Mosses are more conspicuous with *Mnium hornum* and *Hypnum cupressiforme* the most frequent.

But the origin and structure of this exposed part are the same as for the associates behind, except that the absence of litter and exposure to wind has modified the ground flora.

#### BEECHWOOD.

##### *The consociation nucleus.*

The beech associates, originating either in the coniferwood or the rowan-birch associates, gives rise to a woodland in which the beech by suppressing its competitors becomes dominant and practically pure. Two small examples are

FIG. 7. (Above.) Ground transect along the line *AB* in Fig. 3, from the line of old beeches (*F*<sub>1</sub>)—two of which are shown on the left—into the adult pinewood (with some larch). The frequency of the subsynchronous beech (*F*) decreases with distance from the parents: in their neighbourhood young beech with *Sorbus aucuparia* forms a continuous subcanopy to the pines: to the right and beyond the limits of the figure young beech is rare. *Sorbus aucuparia* and *Betula* spp. are more frequent where the frequency of the young beech is greater, and in gaps, for example between the pioneer beeches, birch colonises freely. Subspontaneous larches are common but many are dead or dying. The absence of pine regeneration is to be noted.

(Below.) Profile transect along the broken line through a relatively open part of the wood showing the stem and crown forms of the trees and their relative positions.

found in which the process has taken place, one belonging to Type 1 (Fig. 1) in which beechwood replaces the rowan-birch associates, the other belonging to Type 2 and having its origin in the coniferwood (Fig. 2). The two are considered together.

Although a majority of the beeches are fairly tall and of similar size, some are younger and grow up in gaps not hitherto fully stocked with beech. The tallest reach 64 ft. (19.5 m.) (Type 1) and 71 ft. (21.7 m.) (Type 2) and are probably in late middle life, the former from their appearance being younger and likely to grow taller. The stems are relatively straight and free from branches. Occasional living and dead birch and pine are found in the respective examples and in both relicts of the shrub layer are seen in the occasional dead rowans. Seedling beeches are occasional to frequent and may survive the third year.

In both the ground is for the most part without plants. In Type 1 the subsidiary vegetation is represented by sparse *Anemone*, *Oxalis* and *Luzula pilosa*: mosses by *Mnium hornum*, *Plagiothecium undulatum* and *Polytrichum formosum*. The humus is 5 cm. thick and no layer of *Vaccinium* rhizomes is visible, but on digging dead rhizomes of *Pteridium* are found.

In Type 2 the most prominent plant is *Vaccinium* (f.—a.) which is small (occasionally up to 15–20 cm.) with leaves subnormal in size. *Deschampsia* is occasional and found only on stumps, boulders, etc. *Luzula pilosa* is also occasional. With the exception of *Polytrichum* spp. and *Hylocomium triquetrum*, which grow up through the leaf litter, all the mosses are found on knolls. The beech humus is from 7.5 to 10 cm. thick, the upper layers laminated, the lower more decomposed. Below this are found *Vaccinium* rhizomes and a layer of structureless peat 2.5–3.8 cm. thick.

It is thus clear that owing to the thickness of the slowly decomposing beech leaf humus, there can be no *Deschampsia* stage in the life history of the sheltered pure beechwood (Type 2). In Type 1 on the other hand there is likely to be an *Anemone-Oxalis* stage before maturity is reached.

#### *The adult beechwood.*

No subspontaneous adult woods exist in this neighbourhood, but it is assumed that the consociation nuclei will develop a structure and floristic composition similar to the four small planted beechwoods now described. In two of these the beech has been planted with conifers (now mostly removed or suppressed so that the beech is almost pure) and two are strips marginal to *Deschampsia* shelterbelt woodlands and represent the mature structure of these.

There are only fifty-seven species in all—thirteen woody plants, of which six are native, twenty-five herbs, grasses and dwarf shrubs and nineteen bryophytes. This total is only a little over one-half of the number found in the adult coniferwood, felled area and rowan-birchwood. Beech of course is dominant, rowan coming next with an average frequency of 3.9. In the ground

vegetation *Vaccinium* dominates. Despite the leaf litter, held in place by *Vaccinium*, *Deschampsia* has a high average frequency (4.0), a result due to the support which its long leaves receive from the *Vaccinium* stems and to the fact that the vigour of *Deschampsia* is actually increased by beech leaf litter when its leaves can rise above it. A similar effect is seen in *Holcus mollis* with an average frequency of 2.9—a figure higher than that recorded from any of the heathwoods described. The other species listed on p. 341 have for the most part an average frequency less than that found in the coniferwood, felled area or rowan-birchwood. Among bryophytes the only species with a high average frequency is *Hylocomium triquetrum* (3.0), the rest having values of 2.0 or less and usually less than those recorded from the earlier stages of the succession. It may again be pointed out that no species is exclusively found in the beechwoods, and that all occur in one or other of the communities already described.

#### *Life form.*

The spectra of the beechwoods are characterised by the absence of therophytes and a high percentage of chamaephytes.

	P.	Ch.	H.	G.	T.	Total		
All species (excluding planted conifers)	24.5 (9)	16 (6)	46 (17)	13.5 (5)	0	100 (37)		
	Ch.	H.r.	H.s.	H.c.	G.r.	G.rad.	T.	Total
Ground vegetation (all species)	21.5 (6)	18 (5)	14 (4)	29 (8)	14.5 (4)	3.5 (1)	0	100.5 (28)
		61 (17)			18 (5)			

The affinity of these beechwoods to the heath communities among which they have been planted is brought out by the close correspondence of the data (p. 333). It is to be noted, however, that the rosette and caespitose hemi-cryptophytes increase their relative numerical strength in the beechwoods.

The height and form of the beeches vary: in the shelterbelts they have clean straight stems, in the coniferwood relatively wide-spreading crowns and no great height (about 65 ft. or 20 m.). Besides the planted adults, occasional to locally frequent subspontaneous young beech is found. The height of the rowan increases with distance from the beech stems, being small (about 30 cm.) directly under the beech crowns and increasing to 10 ft. (3 m.) in opener parts between them. *Vaccinium* varies in the same way with an average height of about 25 cm.

#### *Structure and life history.*

The examples are relatively open—a plot of 10,000 sq. ft. containing only thirteen adult beech, one young beech, two small oaks (the taller 46 ft. or 14 m.) and one larch (59 ft. or 18 m.), so that the rowan shrub layer although varying in height is fairly well defined. The dwarf-shrub layer of *Vaccinium* is continuous and herbs and grasses are inconspicuous by contrast. The layer of bryophytes is practically suppressed by the beech humus (10 cm. deep),



under which, in the adult shelterbelt beechwood, *Deschampsia* remains are found.

These four woods have been planted, but they may be taken as representing the adult condition of the subsponaneous consociation nuclei. The normal development of these nuclei would therefore show a floor at first almost destitute of plants until *Vaccinium* made its appearance, when with further opening out of the canopy a shrub layer of rowan would be added to the continuous carpet of the *Vaccinium* dwarf-shrub layer—a structure identical to that found in the adult pinewood.

The presence of young beeches of varying age shows that germination and establishment conditions are suitable to the beech, and indicates the possibility of the present planted adult woods being succeeded by subsponaneous beechwood.

Representing the adult condition of Type 1, there is one example of an open beechwood on ridged soil, whose structure is similar to that described. The floristic composition, however, differs by the presence of *Anemone* (o.—lf.) and the higher frequency of *Oxalis* (f.—a.) and *Pteridium* (m.l.a.). It is of interest to note that in the hollows between the ridges the remains of both *Deschampsia* and *Holcus mollis* are found below the accumulated beech litter.

Putting together therefore the facts relating to the beech associates, consociation nuclei and this adult beechwood, the life history of Type 1 beechwoods would show an *Oxalis-Anemone* stage followed by one of *Vaccinium* (with *Anemone*).

In the adult beechwood, young beeches are locally frequent but are kept down by the grazing of cattle.

#### THE STATUS OF THE VEGETATION AND ITS FATE.

The contrast between the historical records of the vegetation and what exists now is eloquent testimony to the labours of past generations of the rural inhabitants of Aberdeenshire; and it is not commonly realised that much of this change is relatively recent (p. 323). By trenching, draining and the removal of boulders, heath has been converted to arable land and plantations made with little soil preparation except the essential one of drainage. Under present conditions the open drains are much neglected, and in many cases cease to perform their function adequately, but the fact that the woodlands are small and in most examples adjoin arable land, the maintenance of whose fertility depends upon good drainage, to some extent mitigates the evil effects resulting from neglect and retards retrogression to heath.

The lack of pine regeneration in the coniferwood prepares the way for a speedy retrogression: and when next the pine appears it is as a colonist of heath. The removal of trees by clear felling has as a result the re-establishment of heath, aided no doubt by the raising of the water table; but by the gradual and selective felling of the conifers this process of retrogression is retarded

by the interpolation of a rowan-birchwood. Thus these woodlands of pine and rowan-birch owe their existence and maintenance to human activity, the former by planting, the latter by a method of woodland exploitation—and both by drainage. Left to themselves reversion to a heath with scattered pines, rowans and birches would take place. The fate of the beechwoods is discussed below, but it is held that they are unable to maintain themselves indefinitely and that reversion will take place. Further, beech is apparently unable to colonise undrained heath.

The vegetation described is therefore post-climax and maintained by man.

From evidence outside the four areas described it is concluded that on Type 1 soils on Deeside there is a natural succession from heath through birchwood to oakwood. Here, in the neighbourhood of Aberdeen, the evidence is in favour of beech attaining a more permanent footing and forming the climax.

The question of the status and influence of the beech is a matter not only of purely academic interest but to foresters of great practical importance, and although pure beechwood is of small extent, with a short history behind it, yet some discussion on the evidence of its permanence and the part it plays on this soil (Type 2) is desirable.

The account of the growth and development of the beech in the rowan-birchwood and coniferwood, culminating in the appearance of the consociation nucleus, clearly shows that the existing conditions both in the coniferwood and the rowan-birchwood have been and are satisfactory for beech establishment. Further the existence of young beech in the adult beechwood gives promise of a subspontaneous wood replacing the present planted one and suggests the possibility of beechwood being self-reproducing and stable.

Against the possibility of its permanence one important fact has to be borne in mind. In our oceanic climate and on this soil type the bulky beech litter does not readily decay and by accumulation forms a thick laminated humus which does not become incorporated with the mineral soil below. This accumulation will go on so long as a beech canopy is maintained, and the litter settling down sets up conditions favourable to leaching and hostile to soil aeration and normal growth of the tree (cf. Part I, p. 152). In this way it is believed that the beeches would gradually die out and give place to a heath vegetation capable of growing under the unfavourable conditions: and this result, being due ultimately to the soil's reaction to leaf litter and to the local climate under the beech canopy, will take place whether man's present influence is maintained or not.

The formation of an undesirable raw humus under beech is by no means confined to the north, but occurs also in the south, where, on soils with a distinct podsol profile and bearing the "oak-birch-heath association," a black felt of dry peat (Trockentorf, mor) is commonly found.

The conclusion that beech induces soil degeneration leads to a qualified acceptance of the text-book (German) teaching on the use of beech for under-

planting light-demanding trees on poor soils. In Central Europe beech is regarded as a "soil improver" in virtue of certain qualities which ameliorate both the physical and chemical conditions of the soil. Now this beneficial action of the beech is conditioned by climatic and soil factors (among which the  $\text{CaCO}_3$  content is important (12)) which, over wide areas on the continent, form a complex optimal for the object in view, but which in this country is suboptimal and on certain soils, definitely harmful. A full discussion of the rôle of beech in silviculture and of the ways in which beech acts on the soil would be out of place here, but it is interesting to record that the experience of foresters in north-east Scotland and in northern England (30) is diametrically opposed to the imported and unqualified German teaching and is in harmony with the position stated above and with the experience of foresters in the northern countries of Europe, e.g. Müller (16). It is thought that this may also be true even of beech (? native) in south-east England.

These remarks apply to beech in continuous canopy and not to the use of occasional beeches in coniferous woods.

The persistence of beech as the climax on Type 1 soils is doubtless of longer duration, but even here, although litter decay is more rapid, it may be questioned if beech is permanent over an extended period. In some of the beechwoods of the Chiltern Hills plateau a thin but definite bleached horizon is found; and in Sweden, Lundblad (15) has shown that under a beech canopy a brown earth soil may degenerate. Thus by a change in the local climatic conditions due to a beech canopy the rate of humus decay is depressed, humus accumulates, leaching is accentuated and the soil degenerates.

#### SUMMARY.

The introduction of the beech to Scotland and its subsequent widespread use in the formation of shelterbelts to protect crops and stock emphasise the lack of native trees suitable for the purpose. The beech has been planted throughout the lowlands of Scotland, sets seed as far north as Caithness (lat.  $58^\circ 30'$ ) and in Strathdon (lat.  $57^\circ 10'$ ) survives up to an altitude of 1350 ft. (411 m.), although seedlings have not been seen at an altitude higher than 700 ft. (213 m.)—lat.  $57^\circ 18'$ . Thus the climate of the lowlands of northern Scotland is quite suitable for its growth and reproduction, followed, where opportunity offers, by establishment and successful competition with native and alien trees.

In Part I an account is given of the shelterbelt beechwoods commonly planted in strips in exposed situations throughout the north-east of Scotland. There are two types of these, the *Deschampsia* type and the *Holcus* type, named after the grasses *Deschampsia flexuosa* and *Holcus mollis*, respectively dominant in the ground vegetation. Their floristic composition, structure, biological spectra and habitats are compared and the main differences noted

are found to be correlated with the degree of exposure to the prevailing south-west winds. In very exposed shelterbelts the leaf litter is blown away; *Holcus*, in these circumstances, is unable to compete successfully with the beech roots, and *Deschampsia* forms a mat: in less exposed situations or in the more sheltered parts of exposed shelterbelts, the low-growing *Deschampsia* mat is absent or is covered and killed by the beech leaf litter; and *Holcus*, whose leafy erect shoots help to retain the litter, dominates.

Generally the species characteristic of the *Holcus* type find the habitat of the *Deschampsia* type limiting or suboptimal, whilst those characteristic of the *Deschampsia* type are or tend to be excluded by competition with the taller growing forms of the *Holcus* type which help to retain the beech leaf litter.

On steep sheltered slopes and on fertile soil (all the examples investigated grow on soil derived from Old Red Sandstone) beechwoods with a ground vegetation dominated by herbs (*Anemone nemorosa*, *Stellaria nemorum*, *Sanicula europaea*, *Luzula maxima*) are found.

The grassy beechwoods are related to heath and the dry oakwood: the herbaceous beechwoods to the damp oakwood of the lighter loams.

The behaviour of the beech towards the semi-natural vegetation and planted conifer woods of four acres near Aberdeen is worked out in Part II. The affinities of the vegetation on these areas to the heath pinewoods on Deeside are chiefly with the *Deschampsia-Vaccinium* and locally with the *Oxalis-Anemone-Rubus* (*Vaccinium*) types.

The original vegetation, probably heath with scattered pines (*P. silvestris* var. *scotica*), birches and rowans, nowhere exists in its primeval condition, for most of the land has been cleared of boulders, drained, trenched and brought under arable cultivation. Some of what remains has been planted with conifers (chiefly *Larix decidua* and *Pinus silvestris*), and apart from the cutting of a few shallow open drains, now mostly neglected, the soil is left undisturbed.

The soil is a podsol or a podsol-glei, and data respecting its chemical composition, profile, depth and hydrogen-ion concentration are given.

The vegetation is essentially heathy. The coniferwoods on clear felling leave behind a patchwork dominated by *Calluna vulgaris*, *Vaccinium myrtillus* and *Deschampsia flexuosa*. If the felled area is left alone *Calluna* spreads and reversion to heath ultimately follows. A return to dense woodland apparently does not take place, but scattered subspontaneous pines appear and form a pine-heath. If, on the other hand, the coniferwood is selectively and progressively felled the shrub layer of rowan together with spontaneous birch forms a rowan-birchwood. The fate of this is uncertain, but there is evidence for the belief that this also reverts in time to a *Calluna* heath, although the retrogression is delayed.

Wherever beech adjoins coniferwood or rowan-birchwood invasion takes place and beechwood results. Beech, however, is unable to colonise the ground which has reverted to *Calluna* heath.

The inability of spruce (*Picea excelsa*) to regenerate is of interest, because northern Scotland is a vegetational outlier of the Evergreen Coniferous Forest of northern Eurasia.

Some factors influencing the succession and the competition between the more important species are next discussed. The taller growing and more shade enduring beech with its accommodating root system competes successfully with the pine, larch, birch and rowan. In the life history of the even-aged coniferwood a *Deschampsia* stage is followed by one of *Vaccinium*. In this sequence the light needs of the succeeding dominants is important, but tree-root competition affects the vigour and flowering of the *Deschampsia* though it has no influence on *Vaccinium*. In the felled area the mat of *Deschampsia* offers almost insurmountable obstacles to *Calluna* *ecesis* but *Calluna* is able to overcome *Deschampsia* by slow vegetative spread.

These conclusions are applied to the interpretation of the vegetation of the different plant communities next described—planted conifer wood, felled area, rowan-birchwood, beech associates and beechwood.

The analysis of the adult beechwood shows, in its floristic composition, structure and biological spectrum, an essential unity with the neighbouring heathwoods. In particular no species alien to the heathwoods is found, and the subsidiary vegetation consists of those native species which can put up with the new conditions, particularly with shade and deep humus.

The application of the historical and vegetational data to the settling of the status and fate of these woodlands leads to the conclusion that they form a sere leading to a post-climax dependent on the maintenance of human control. The natural tendency to humus accumulation on a podsol in an oceanic climate is accentuated by the depressed activities of the organisms of decay working in a woodland climate whose summer mean temperature must be lowered by the shade of beech. The litter accumulates, forming a thick laminated raw humus hostile to beech regeneration. Beechwood therefore will eventually degenerate to heath: and this seems true for the beechwoods allied to the *Oxalis-Anemone-Rubus* woods of better soils as well as for those related to the *Deschampsia-Vaccinium* pinewoods.

It is a pleasure to acknowledge my indebtedness to the many proprietors for free access to their woodlands—in particular to Sir Sydney J. Gammell of Countesswells. Grateful acknowledgment is also made to the Carnegie Trust and to the Royal Society for financial assistance. Finally, I again wish to place on record my deep indebtedness to Professor Tansley.

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# SKETCHES OF THE VEGETATION OF SOME SOUTHERN PROVINCES OF SOVIET RUSSIA

By WILLIAM SEIFRIZ.

## INTRODUCTION.

KNOWLEDGE of plant life in the southern countries of the Union of Soviet Socialistic Republics<sup>1</sup> is accessible to the outside world in the form of several classical Russian and German works, but these are none too familiar, and they leave some interesting territory untouched. Furthermore, Russian taxonomists and ecologists have been very active since the Revolution and have brought together many new facts. It seems, therefore, worth while to present, in English, an account of the flora of certain southern Soviet provinces, and thereby bring together some of the newer researches now scattered in relatively inaccessible journals, to which are added a few original observations of my own.

I had the pleasure, in the summer and fall of 1929, of leisurely journeying from the Crimea to within 100 miles of the Chinese border in Turkestan. The present paper is the first of a series in which the botanical results of this excursion are described. The regions visited were the Crimean Mountains, the Georgian Military Way (North Caucasus), the Bakuriani Basin (Minor Caucasus), the desert at Repetek (Kara Kum), and the Transilian Mountain range of Kazakstan (eastern Turkestan).

My sojourn in these southern states of the Soviet Union was made in company with a number of Russian botanists who either travelled with me for a time or resided in the places where I stopped. I am indebted to them all and I shall express my appreciation in these articles; but to certain of these companions special thanks are due. I am grateful to Prof. N. A. Maximov who gave to my stay in Russia the necessary official backing; to Mrs Tatiana Krasnosselsky Maximova, who, with characteristic initiative and energy, helped our expedition through many trying experiences, and who has since effectively obtained for me much information necessary to the satisfactory completion of these articles; and to Prof. Venedict Kolesnikov who was my companion in the Crimea and North Caucasus. I am also grateful to Dr Forrest Shreve, of Tucson, Arizona, for his courtesy in reading the manuscripts of these articles, and to Mr Paul Bausch for kindly making a number of drawings, including Fig. 3 of the present article.

<sup>1</sup> Many encyclopaedic and geographic references give "Union of Socialistic Soviet Republics" as the name of the present Russian Union. The Russian bank notes have "Union of Soviet Socialistic Republics" printed upon them.

## I. THE ALTITUDINAL DISTRIBUTION OF PLANTS ON THE CRIMEAN MOUNTAINS

(With Plates XIV-XVII and three Figures in the Text.)

The success of the botanical study of the Crimea here presented is largely due to Mr V. F. Vasiliev, upon whom rested the final identification of all plants collected. Mr Vasiliev, with typical Russian courtesy, planned and conducted the trip into the mountains. His published accounts<sup>1</sup> of the Crimean flora have been of great help in the writing of this article. I am further indebted to Mr N. V. Kovaliev, Director of the Nikita Gardens, for officially assuming half of the responsibility of the trip.

### THE FLORA.

Plant geography is an old subject. The evident and superficial things have been done. To add anything of fundamental significance now requires years of intensive and extensive work which must be left to those residing in the country. The chance visitor can grasp only something of the outstanding botanical features of the region; his glimpses assume a more substantial nature, and become of some real value, only when he has the help of the taxonomic specialists of the country.

The Crimea, or Krim, is a peninsula projecting into the Black Sea from the south coast of Russia. A very narrow strip of land saves the Crimea from being an island which it more resembles. It is of irregular shape, considerably broader than long. The 45th parallel passes across the peninsula, dividing the Crimea into two geographically distinct regions, the southern mountainous coastal strip, 30 miles in width, and the broad northern steppe which constitutes more than two-thirds of the total area of the state. The capital, Simferopol, is a few miles south of latitude 45°.

The Crimean Mountains attain their maximum height close to the coast (Fig. 1). Here they rise to an altitude of 1500 m. within 8 km. of the shore. At one point an altitude of 1200 m. is reached within 3 km. of the shore; this is the peak Ai-Petri. It is impossible to refer to individual mountains in the coastal range, as the top is one extensive plateau known as the Yaila. The main portion of the plateau is some 30 km. in length, varying from  $\frac{1}{2}$  to 5 km. in width. The highest point, with an altitude of 1540 m., is toward the eastern end, just above the town of Yalta<sup>2</sup>.

<sup>1</sup> "Die Vegetationsverhältnisse der Gegend Sudak-Alushta" (published in Russian with a German summary). *Journ. Gov. Bot. Gard. Nikita, Yalta, Crimea*, **10** (2), 1928.

<sup>2</sup> The spelling of Russian words has been much influenced by German translations and by historical traditions. The transliterations adopted here aim not only at correct pronunciation, but also at retaining the Russian spelling in so far as this is possible. Pronunciation is of greater importance than spelling, and where it is necessary to change the latter to achieve the former, I have done so. There are naturally certain minute shades in pronunciation which only Russians

Crimea's coast has long been famed as Russia's riviera (Fig. 1). The largest of the south-coast towns is Yalta. Several miles east of Yalta are the Nikita Botanic Gardens, consisting of 500 acres extending up from the shore to the village of Nikita. Immediately above Nikita rises a high spur which projects southward toward the coast from the main Yaila plateau (Fig. 1).

The journey into the mountains leads from the Nikita Gardens up along the west slope of what I shall call the Nikita spur, over the Yaila plateau, and part way down the north side of the coastal range to the former monastery of Kozmo Damian where the night is spent. The return trip may be made by way of the east slope of the spur.

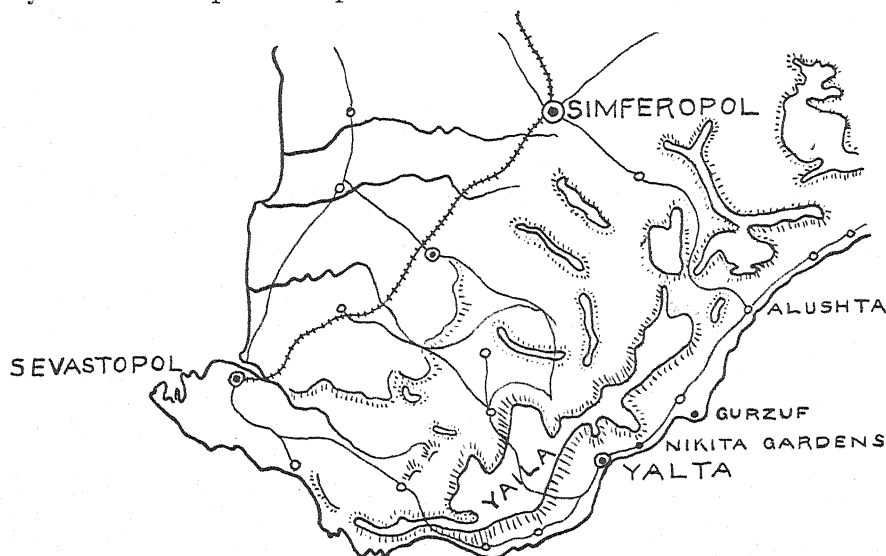


FIG. 1. The southern tip of the Crimea showing the Yaila plateau.

The Crimea lies in the southern part of the temperate zone with only the suggestion of a tropical flora. Ripe figs, *Ailanthus*, and the leguminous tree *Albizzia*, together with a hot and dry summer, remind one of the Near East, but the absence of cultivated palms and the scarcity of citrus fruits indicate that the Crimea has a winter not tropical in nature. The average summer (August) temperature at Nikita is  $24.6^{\circ}\text{C}.$ , and the winter (January) tem-

can accomplish. It seems best, for English readers, to use "j" for the sound of "s" in "pleasure," and "y" for the Russian й, the sound in the pronoun "ye": thus "Yalta" and not "Jalta" for the Crimean seaside town. Whether to use "v," "ff" or "w" for the familiar ending to many Russian words is a question which is answered as one wishes. The Russian letter which ends words of this sound is "b." This is not our "b," for which the Russians have another letter, but our "v." Since "v" gives the sound fairly well, it is the best of the three possible transcriptions, as it conforms not only to pronunciation but to Russian spelling. For the same reason I much prefer "Buchara" for the Turkestan city to the familiar English transcription "Bokhara," which gives neither the Russian spelling nor the Russian pronunciation. The addition of "c" in "Buchara" is necessary to approach more closely to the Russian pronunciation.

perature 4° C. The rainfall at sea-level on the southern coast (Nikita) is 50 cm. a year (on the northern steppes it is but 30 cm.) and on the mountain tops, the high Yaila plateau, it is 120 cm. The yearly distribution of rainfall in the Crimea is irregular. On the steppes in the north, summer rains are continental in character and constitute 43 per cent. of the total annual amount. In the mountains, the yearly distribution is more uniform, with spring and summer maxima. On the southern coast, 56 per cent. of the total annual precipitation falls from October to February and 24 per cent. from May to August. So dry a spring has a marked influence on the character of the vegetation of the coast.

The Crimean mountains rise abruptly from the south coast, leaving but a narrow strip of land suitable for cultivation. Relics of a former forest are still present here, but most of the area is cultivated, being planted chiefly with grapes and tobacco. This coastal agricultural strip constitutes the first of the five zones into which I have divided the southern slope of the Crimean mountains.

#### ZONE I. THE COAST (0-300 m.).

*Juniperus excelsa* is the only tree which forms pure stands along the southern shore of the Crimea. Here and there small woods of a pure *Juniperus* growth still persist, left-overs from an extensive forest which has long since been cut. The juniper grows on poor rocky soil to the almost complete exclusion of other coastal trees such as the oaks. Five species of *Juniperus* occur in the Crimea, *J. excelsa*, *J. oxycedrus*, *J. depressa*, *J. foetidissima* and *J. sabina*; the last is found on the higher mountain peaks. Of these species *J. excelsa* is by far the most abundant. *J. oxycedrus* is the only other juniper occurring in the first zone in any quantity and it is not frequently seen. This last species is of interest because it ordinarily exists as a low shrub, yet it may develop, when given time, into a substantial tree. (Wulff<sup>1</sup> gives a sixth species, *J. isophyllos*, as occurring along the coast with *J. excelsa*.)

Two other trees, *Quercus pubescens* and *Carpinus orientalis*, join *Juniperus excelsa* in characterising the coastal region. Of these three only *Juniperus* is limited to the first zone. *Quercus* and *Carpinus* also occur further up if they can find space in areas deforested of pine and beech.

Other oaks occurring in the Crimea are *Q. sessiliflora* at higher altitudes on the southern slope, and *Q. pedunculata* chiefly on the northern side of the mountains. These two species are very much alike. A second *Carpinus*, *C. betulus*, reaches the tree line.

*Acer campestre* is a not infrequent inhabitant of the coastal region. *A. hyrcanum* is a high-altitude species. *Fraxinus excelsior* and occasionally *F. oxycarpa* are found in the first zone. *Arbutus andrachne* is a conspicuous tree of the coast because of its bark, which is smooth, of a rich reddish brown colour, and constantly peeling. The tree is at home in the Crimea and Asia Minor.

<sup>1</sup> E. Wulff. *Vegetationsbilder aus der Krim*, Jena, 1926.

There are a large number of wild pear, apple and cherry trees in the Crimea; *Pirus elaeagnifolia* is one of the most common of these. The closely related species *P. communis* may attain great age. Equally abundant is the wild apple, *Pirus malus* (*Malus communis*); somewhat less frequent is *Prunus spinosa*, and the wild sweet cherry *Prunus avium*.

Chlorosis is of unusual occurrence among the fruit trees of the Crimea, both wild and cultivated forms, especially the pears, due to a strong alkaline soil.

*Pistacia mutica* (Anacardiaceae), the turpentine tree, though but occasionally seen, is a true representative of the flora of the Crimea, as it is also of that of Italy. The most historic representative of this species, at Nikita, was seen by Engler in 1900; he estimated its age as 1000 years.

An interesting shrub is *Paliurus spina Christi*, one of the Rhamnaceae, a Mediterranean and Near East genus. The plant attracts attention because of the broad fringe or wing on the fruits.

Occurring very abundantly along the coast is *Ailanthus glandulosa*. It is usually found as a rank-growing roadside weed some 4 to 6 ft. in height, but if given the opportunity it reaches tree size and forms a striking feature of the landscape when bedecked with its large clusters of red fruit in late August.

The ubiquitous *Rosa canina* is abundant along the coast, extending up into the mountains.

Among the herbaceous plants certain species grow so profusely that they conspicuously characterise the coastal vegetation. This is especially true of *Clematis vitalba*, the only species of this genus in the Crimea. It grows in great luxuriance. The plant is distributed not only throughout southern Russia and the Mediterranean region, but extends, as is well known, north-westwards through Europe to southern England. I was interested in finding *Clematis* abundant and in rich full flower keeping company with *Artemisia* and *Alhagi* in the Kizil Kum desert near the Aral Sea. Dr Shreve informs me that *C. ligusticifolia* is common in the Arizona deserts, with *Atriplex* occurring on the alkaline flood plains.

*Euphorbia biglandulosa* is widely spread in the Crimea along the coast; in Greece it covers large waste areas. Along the shore grows *Asphodeline lutea*; *A. taurica* is another Crimean species of this genus. *Iberis taurica* (Cruciferae) is an endemic, occurring in stony areas.

Numerous world-known herbaceous plants occur by Crimean roadsides. *Cichorium intybus* is a frequent reminder of American fields. *Verbascum* is represented by numerous species. Leguminous plants, such as *Spartium junceum*, are abundant, as also the Cruciferae. Five Papavers occur in the Crimea. They are regarded as weeds and are of wide distribution, occurring from the coast to alpine pastures. *Ranunculus* is well represented.

The orange-coloured *Crocus susianus* is found along the coast near Nikita, with its cousin, the brilliant purple-flowered *C. speciosus*. *Scilla autumnalis*

and *Stachys iberica* are other low-altitude forms. *Ephedra vulgaris* is at home here; it is found just south of the 45° parallel from Spain to eastern Turkestan. There are some fifty species of grasses in the Crimea, *Festuca sulcata* and *Hordeum bulbosum* being common at Nikita. Fifteen Carexes occur. That world-wide species, *Equisetum arvense*, is also present. Ferns are not numerous, only three genera and four species existing on the peninsula.

Introduced plants which have become wild, together with those maintained by cultivation, often distinguish the floral topography of a country more than do the native plants. This is especially true in a densely populated region where intense agriculture is pursued. Exotic plants are the result of man's work, and man is usually omitted as a factor in "natural" plant distribution. The landscape of the Crimean coast is more strikingly characterised by introduced and cultivated plants than by the native species. To omit mention of the tall and stately *Cupressus*, of *Cedrus*, and *Albizzia*, would be to fail to give an accurate picture of the Crimean coastal flora. The symmetrical cypresses are conspicuous along the southern coast. Among the occasional exotics are the two superb cedars, *Cedrus atlantica* and *C. libani*. The leguminous tree *Albizzia* (*Acacia*) *julibrissin* is extensively planted as a shade and decorative tree. It does well along city streets because of its drought-resistant qualities. When in flower it is most decorative. The tree is a native of Trans-Caucasia and China.

*Quercus suber* is now being introduced with the ultimate intention of making Russia independent of Spain in its need of cork. Ripe figs, *Ficus carica*, add a subtropical touch. *Punica granatum* is likewise grown. The cultivated *Citrus trifoliata* is the only citrus plant in the Crimea.

The two most extensive crop plants are tobacco and grapes. "Dubek" is the Tartarian name for the finest of Russian tobaccos. It is grown in the Crimea.

"Vinograd" or "wine bunches" as the Russians call grapes, constitute the chief agricultural product of southern Crimea. Vineyards cover many of the lower mountain slopes (Pl. XVI, Phot. 5). The scientific study and control of Crimean grape culture and wine production is in the hands of the Experimental Station at Nikita Gardens. A total of 800 varieties of grapes from all parts of the world are grown here. Of this number, 670 belong to the species *Vitis vinifera*. The grapes are converted into wine in the Station's own cellars, which have produced some of Russia's best wines for more than a century. Through the courtesy of the Director, Mr M. A. Gerasimov, the vineyard and cellars may be visited. The varieties of wines produced here are numerous, from the usual "vin ordinaire," to Malbeck, Bordeaux, Madeira, and the selected Muscat rouge de Frontingant, acclaimed the finest wine of the world, though another connoisseur gives preference to the equally soft and sweet Muscat noir d'Alican (Caillaba). Very fine also is Bastardo 26 from Spanish grapes; its flavour is more distinctive and less sweet, though still soft. Russia



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hopes to replace France in the production of Muscat owing chiefly to the destructive work of *Phylloxera vastatrix* in the latter country.

One article of food commonly sold along the southern coast, but grown in north Crimea, is of interest to Americans as a contribution of their continent to Europe; it is "corn on the cob." Children peddle it cooked, ready for eating.

Still another plant which is widely grown is the sunflower; the seeds are eaten, though chiefly used for extracting an oil which constitutes the main cooking and table oil of Russia.

### ZONE II. THE *PINUS LARICIO* BELT (300–800 m.).

The Crimean pine, *Pinus laricio* var. *pallasiana*, forms a belt on the southern slope of the Crimean mountains at an average altitude of about 500 m. The association is a nearly pure one (Pl. XIV, Phot. 1). This pine rarely gets as low as the seashore nor as high as the plateau.

The forest floor of the *Pinus laricio* association harbours little vegetation except for small patches of *Dryopteris filix-mas*, one of the few Crimean ferns. In open areas an occasional *Pirus elaeagnifolia* and *P. communis* are found. It is here that the oldest of the wild pear trees occurs, estimated to be over 200 years. *Ruscus aculeatus* grows in the more open areas of the woods. On the edges of the forest above the village of Gursuf one may find *Saxifraga irrigua*. Other herbaceous species occur in this zone, but they are more typical of the adjoining higher region.

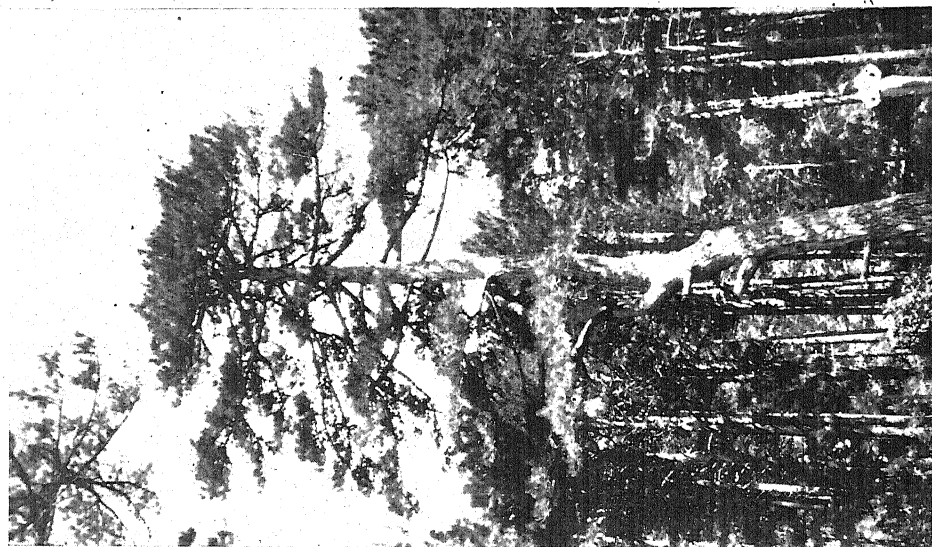
The second zone is essentially a pure stand of the indigenous Crimean pine which has received the name *P. taurica*, though it is perhaps better called by its older name. (Tauria is an ancient name for Crimea.) Many of the pine trees attain very good size and constitute the monarchs of the native flora on the south coast (Pl. XIV, Phot. 2).

### ZONE III. THE UPPER HERBACEOUS REGION (800–1000 m.).

The third zone possesses the two characteristics necessary to form a good herbaceous undergrowth, open woods and ample moisture. This latter condition is maintained by abundant and hard rains, close-hanging clouds, and an absence of desiccating winds. (We recall that the annual rainfall at Nikita Gardens, at sea-level, is 50 cm., while on the Yaila plateau, at 1500 m., it is 120 cm.)

Several new trees appear above 800 m.; most of the lower altitude ones remain. Two of these new members characterise the arboreal vegetation of the third zone; they are *Pinus silvestris* and *Fagus taurica*. The former, the most widespread European pine, is here intermixed with *P. laricio* var. *pallasiana* (*P. taurica*) from the second zone.

In addition to these two species of pine, a third occurs elsewhere on the south coast of the Crimea, *Pinus pithyusa* var. *stankeviči*, a close relative of the Caucasian *P. pithyusa*.



Phot. 2. *Pinus laricio* var. *pallasiana* (*P. taurica*).



Phot. 1. Stand of *Pinus laricio* var. *pallasiana* at  
500 metres.

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*Fagus*, more abundant on the north side, forms small pure stands at high altitudes on the south slope, especially on south-eastern expósures where there is good soil. The two pines are restricted to south-western rocky areas. The beech is so much more typical of the northern slopes of the mountain range, where it forms pure forests miles in extent, that we shall leave further consideration of it until later.

A very few scattered specimens of the yew *Taxus baccata* are to be found in these high rocky regions.

Another species of *Carpinus* appears in the third zone, *C. betulus*, a tree more typical of central and western Europe where it is quite common. The widely distributed European oak, *Q. pedunculata*, is also here at 900 m., but it is not restricted to this altitude. Another new species in this region is the maple *A. hyrcanum*. The northern and high altitude tree, *Populus tremula*, is scattered in the open areas of this zone, though it is not a typical Crimean tree. *Fraxinus excelsior* is still present. *Cornus mas* with its brilliant red berries may likewise be found. Its distribution is also very wide.

To one familiar with south Russian plants, it would be a notable omission if *Sorbus aucuparia* were not mentioned as a high-altitude species. This small tree, which reaches the tree line throughout the Caucasus and again appears in the mountains of eastern Turkestan, is to be found in the Crimea but it is not abundant. It is a relic of the glacial age. The plant occurs in the third zone between 850 and 900 m. altitude. A second species of this genus, which is much more numerous in the Crimea, is *Sorbus torminalis*, so strikingly distinguished by its leaves from its cousin, *S. aucuparia*. This plant is rather common, and while growing best at 700–1100 m. altitude, it is to be found from the coast to, or near, the tree line. There are nine species of *Sorbus* in the Crimea, including *Sorbus aria*.

*Pinus silvestris* and *Carpinus betulus* are the distinguishing trees of the third zone, but the arboreal vegetation characterises the zone less than does the succulent undergrowth. An open herbaceous zone at high altitude, separating a lower forest of large trees from a higher one of small trees, is generally characteristic of plant zonation on mountain sides; thus Shreve<sup>1</sup> has found such a zone on the mountains of Jamaica and I<sup>2</sup> in Java; we shall find the same at high altitudes in the Minor Caucasus.

Among the herbs of Zone III the following are the most conspicuous in August: *Atropa belladonna*, with its glossy, black berries; the European golden rod, *Solidago virga-aurea*, is another very striking and beautiful plant; *Chrysanthemum parthenium*; *Campanula sibirica* (and another larger species); the umbelliferous *Laserpitium hispidum* (its better known cousin, *Daucus carota*, is found at lower altitudes); two *Centaureas*, *C. jacea* and *C. montana*;

<sup>1</sup> Forrest Shreve. "A montane rain-forest." *Carnegie Inst. Publ.* 199 (1914).

<sup>2</sup> William Seifriz. "The altitudinal distribution of plants on Mt Gedeh, Java." *Bull. Torrey Bot. Club*, 50, 283 (1923).

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the world-wide *Epilobium angustifolium* (not a typical Crimean plant); *Echium vulgare*; *Cirsium incanum*; *Linaria vulgaris* (it is always of interest to find in far corners of the world species identical with those so familiar at home); *Melampyrum nemorosum* (Scrophulariaceae); *Ranunculus polyanthemus*; *Salvia glutinosa*, with its ingenious automatic spring for cross pollination; the endemic, *Melilotus tauricus*; and *Lappa* (*Arctium*) *tomentosa* (Compositae), with huge (maximum 18 inch) heart-shaped leaves. One fern is met with, *Dryopteris filix-mas*.

#### ZONE IV. THE TREE LINE (1000-1250 m.).

As one climbs on to the first shelf of the high Yaila plateau at about 1000 m. or more, there is a sudden change in the type of vegetation. The change may be clear cut or not, depending upon the topography of the immediate surroundings. Alpine plants make their first appearance. Trees are much reduced in size, more irregular in shape, and occur in smaller groups of close formation. Typical *Krummholz* is met with. Here occurs the tree line, formed by *Pinus silvestris* (Pl. XV, Phot. 3) and *Fagus taurica* (Phot. 4); the two species rarely occur together. On the western slope of the Nikita spur the pine alone forms the tree line. On the eastern slope the beech predominates.

The fourth zone does not form a continuous belt, nor is it extensive in width. It consists of scattered areas where the trees of the third zone, more dwarfed in size, get up into the alpine pastures.

The tree line region is essentially composite in character, consisting of small woods and meadows; floristically it is subalpine. Among the meadow plants the typically Crimean umbelliferous *Seseli gummiiferum* and its cousin *S. lehmanni* are to be found, as also the endemic *Cachrys alpina* and *Cistus tauricus*.

#### ZONE V. ALPINE PASTURES (1250-1540 m.).

The Crimean coastal mountains do not rise to peaks but culminate in flat meadows which form one long continuous plateau, the Yaila. Only an occasional small rocky summit is to be found. The Yaila is some 30 km. long with a maximum width of 5 km. and an altitude ranging from 1250 to over 1500 m. The few rocky mounds on top rise to maximum heights of 1526 and 1540 m. The open wind-swept meadows of Yaila form the alpine pastures of the fifth zone. The ground is well covered with grass and herbaceous species. Rock plants such as *Saxifraga* are not numerous.

Before the Soviet Government put an end to pasturing on Yaila, these meadows were overrun by hordes of cattle, with the result that relics of the original Crimean alpine flora were to be found only on rocky summits. The plants are now gradually spreading to the floor of the plateau. Among them is the most striking and picturesque of the alpine flowers on Yaila, the Crimean "Edelweiss" *Cerastium biebersteini*, one of the Caryophyllaceae (Pl. XVI,





Phot. 3. *Pinus silvestris* forming the tree-line at 1200 metres.



Phot. 4. *Fagus taurica* creeping down on the south slope; summit of Yaila to the right.

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Phot. 5. The Crimean coast: pine on the left; junipers, oak, cedars and vineyards below.



Phot. 6. *Sideritis taurica* on the summit of Yaila.



Phot. 7. *Cerastium biebersteini* near the summit of Yaila.

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Phot. 7). It first appears at the tree line (1250 m.) and extends to the highest rocky summits (1540 m.).

The Labiate *Sideritis taurica*, (Pl. XVI, Phot. 6), an endemic, is also a frequent inhabitant of the plateau pastures. This Crimean native gets into the high Caucasus and Asia Minor. *Viola altaica* var. *oreades*, but sparingly found in flower in August, blossoms profusely over the plateau in May. It is a much sought after violet by western gardeners. Abundant also are the genera *Alchemilla*, *Trifolium* and *Festuca*.

#### THE NORTHERN SLOPE.

The north side of the Crimean coastal range has quite a different story to tell. Immediately on leaving the plateau meadows, one enters a dense beech forest, and this forest, an almost pure stand of *Fagus taurica*, extends for many miles, covering all the northern mountain slopes. It is a superb sight, whether one views it from above or from within.

The tree line on the north side is slightly higher than on the south, creeping up to 1300 m. The beech trees at this altitude are low and bent (Pl. XVII, Phot. 8), but they soon, at a lower altitude, become fine tall specimens closely grouped to form a dense forest (Pl. XVII, Phot. 9). At 720 m. the trees attain their best growth with excellent boles 40-50 cm. in diameter and 30 m. or more in height.

The beech forest descends to 500 m., to the foot hills north of which lie the vast steppes which make up most of the Crimea. The change in size of the beech, from its lower limit of 500 m. to the tree line at 1300 m., has been described by Poplawska. Fig. 2 is a modified copy of a drawing made by Poplawska<sup>1</sup>. The figure shows the change which the beech undergoes with change in altitude.

The naming of the species of beech which covers the north side of the Crimean mountains has been an interesting problem now finally solved by Poplawska. The Crimean beech resembles *F. silvatica* of central Europe and was formerly regarded as of this species; it also bears a close resemblance to the Caucasian *F. orientalis* to which species it was later assigned. Poplawska finds that the Crimean beech has flowers as in *F. orientalis*, fruits as in *F. silvatica*, and leaves intermediate in size between these two species. Furthermore, the Crimean beech develops root shoots as does its closer relative *F. orientalis*, which does not seem to be true here of *F. silvatica*. Poplawska, therefore, proposes the new specific name, *Fagus taurica*.

Scattered along the fringe of the beech forest are several species from the southern side of the mountains. The two pines, *P. laricio* and, chiefly, *P. silvestris*, occasionally occur, likewise examples of *Carpinus betulus*, *Quercus pedunculata* and *Fraxinus excelsior*.

<sup>1</sup> Poplawska, H. "Die Buche in der Krim und ihre Variabilität." *Österreich. Bot. Zeitschr.* 77, 23, 1928. See also "Étude sur la variabilité du hêtre de Crimée" (in Russian with French summary), *Recherches sur les Parcs Nationaux* (Leningrad), 1926.

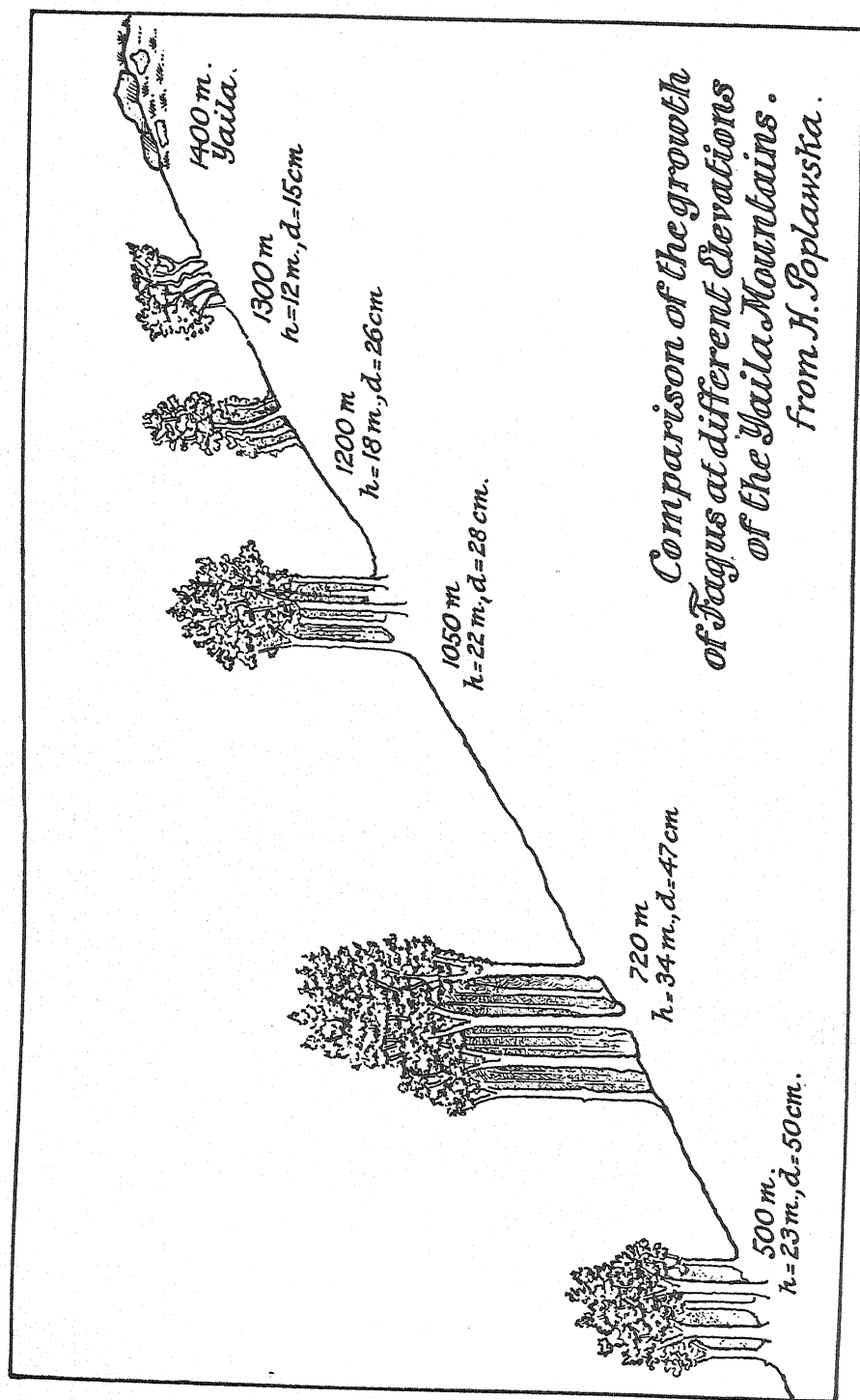
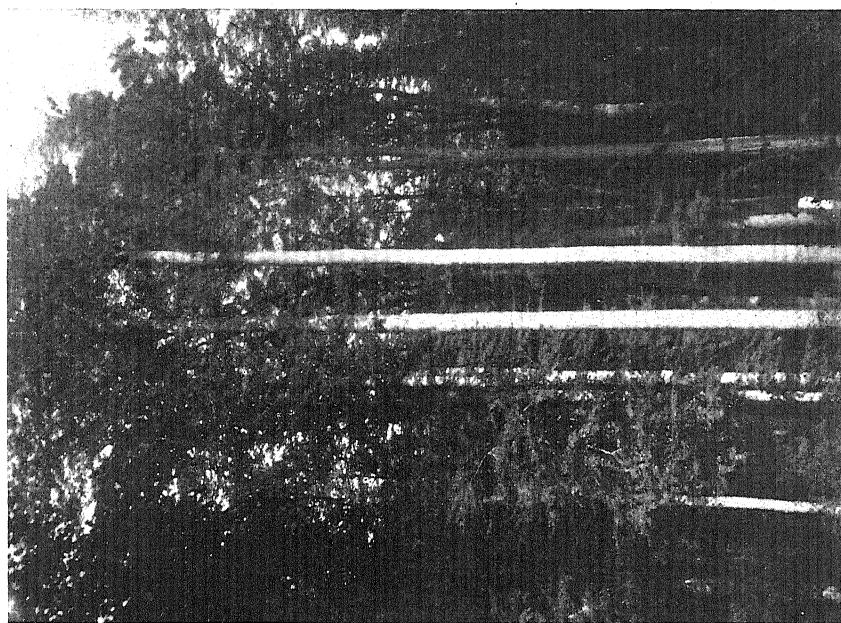
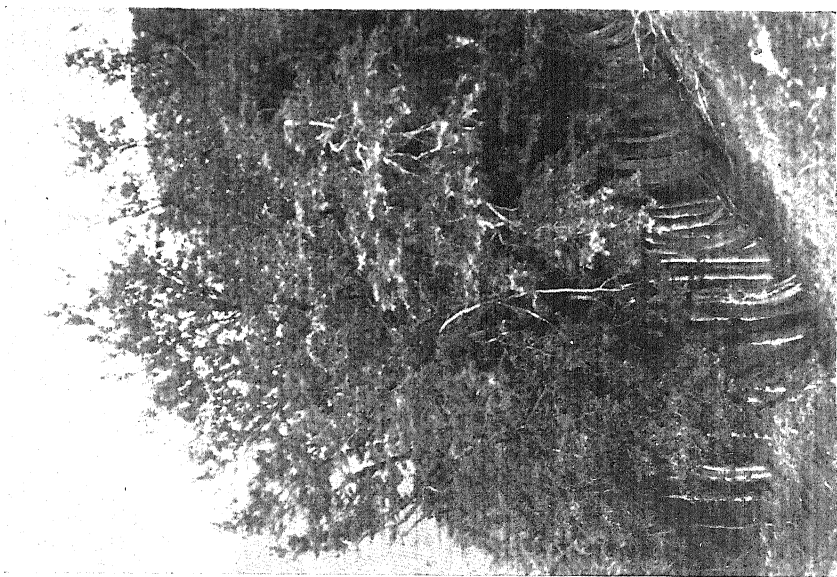


FIG. 2. Change in size of beech with altitude (H. Poplawska).



Phot. 9. *Fagus taurica* forest at 720 metres.



Phot. 8. *Fagus taurica* at tree-line, north slope. 1200 metres.

SEIFRIZ—SKETCHES OF THE VEGETATION OF SOME SOUTHERN PROVINCES  
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MOUNTAINS





The former monastery, Kozmo Damian, situated at an altitude of 650 m. on the north mountain slope, has now been converted into a hospice for travellers. It was formerly frequented by the Czar who used it as a hunting lodge. Here visitors may rest with primitive comforts and meet with other naturalists, for a part of the monastery is a museum and biological laboratory. The former royal hunting reserve is now a national forest. Cutting and grazing are prohibited. Plant and animal life will grow henceforth undisturbed.

#### CONCLUSION.

A good impression of the coarser features of the altitudinal distribution of plants on the southern slopes of the Crimean mountains may be had from the Black Sea directly opposite the Nikita Spur. Fig. 3 is a sketch made a mile off shore and shows, first, the coastal zone, with a *Juniperus* wood isolated

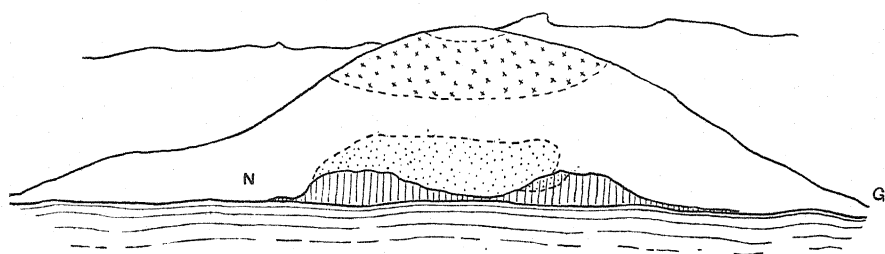


FIG. 3. The Yaila Spur seen from the Black Sea, showing the juniper (dotted), cultivated (white) pine (crossed), and alpine (white) regions: N = Nikita Gardens, G = Gursup.

from scattered *Quercus* and *Carpinus* trees and the cultivated areas; second, the next two zones of pine; and third, the alpine zone. Naturally, at a great distance *Pinus silvestris* is not to be distinguished from *P. laricio*, nor is an herbaceous undergrowth visible.

The Crimea shows great diversity in floral types; its extensive northern steppes are covered, where salty, with *Artemisia*, elsewhere with *Salvia*, *Medicago*, *Onobrychis*, and the grasses *Stipa*, *Festuca* and *Bromus*; on its only slightly less dry south coast grow junipers where the ground is rocky, and oaks in those more favourable areas which have been left untouched by an intensive agriculture; its mountains are covered with pine on the south and dense beech forests on the north; the open woods at upper elevations harbour a rich herbaceous growth; and the high plateaus are carpeted with alpine meadows where the Crimean "Edelweiss" (Pl. XVI, Phot. 7) flourishes.

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# SKETCHES OF THE VEGETATION OF SOME SOUTHERN PROVINCES OF SOVIET RUSSIA

## II. PLANT LIFE ALONG THE GEORGIAN MILITARY WAY, NORTH CAUCASUS

By WILLIAM SEIFRIZ.

(With Plates XVIII-XX, and two Figures in the Text.)

THE Georgian Military Way is the main route across the Caucasus Mountains. It leads from Vladicavcas on the north to Tiflis on the south. The road is famed in Russian history as the scene of many encounters between the Russians and the Gruzini (Georgians). It is equally renowned for its magnificent scenery; the Daryal Canyon and Mount Kasbek are known by name to every Russian school child.

The Georgian Military Way has been trod not only by soldiers but by botanists, with the result that the Caucasian flora is as well known as any in Russia. Some fifty species of plants bear the name *caucasica*. There is a humorous saying among Russian botanists that when in the Caucasus if you do not know the specific name of a plant, guess *orientalis*, if wrong, then guess *caucasica* and you are certain to be right!

The Caucasian Mountains lie diagonally in a north-west to south-east direction across the broad neck of land which joins the Russian Union to Turkey and Persia (Fig. 1). They extend from the Black Sea to the Caspian, and separate Russia proper from Georgia and Azerbaijan. Tiflis is the capital of Georgia, and Baku, on the Caspian Sea, is the capital of Azerbaijan. These two "republics" and Armenia constitute Transcaucasia. The highest mountain in the Caucasus is Elbrus, 5660 m. (18,565 ft.); it lies far west of the Georgian Military Way. Mount Kasbek is second in height, 5043 m. (16,541 ft.), and lies close to the Way. All of the higher mountains are glaciated. Not far from the foot hills of the range on the north is Vladicavcas, a good sized but rather primitive town. Tiflis is the chief city on the south; it lies some 50 km. from the mountains.

The Georgian Military Way, from Vladicavcas to Tiflis, is 220 km. long; the journey over it can be made in a day (10 hours) by auto-bus. More satisfactory for the botanist is to make the journey by carriage from Vladicavcas to Kasbek, which can be quite leisurely done in a day. The remainder of the trip from Kasbek to Tiflis is less interesting both scenically and botanically, and is best made by auto-bus, unless, of course, a survey of the more arid regions on the south side of the mountains is to be included. If one remains

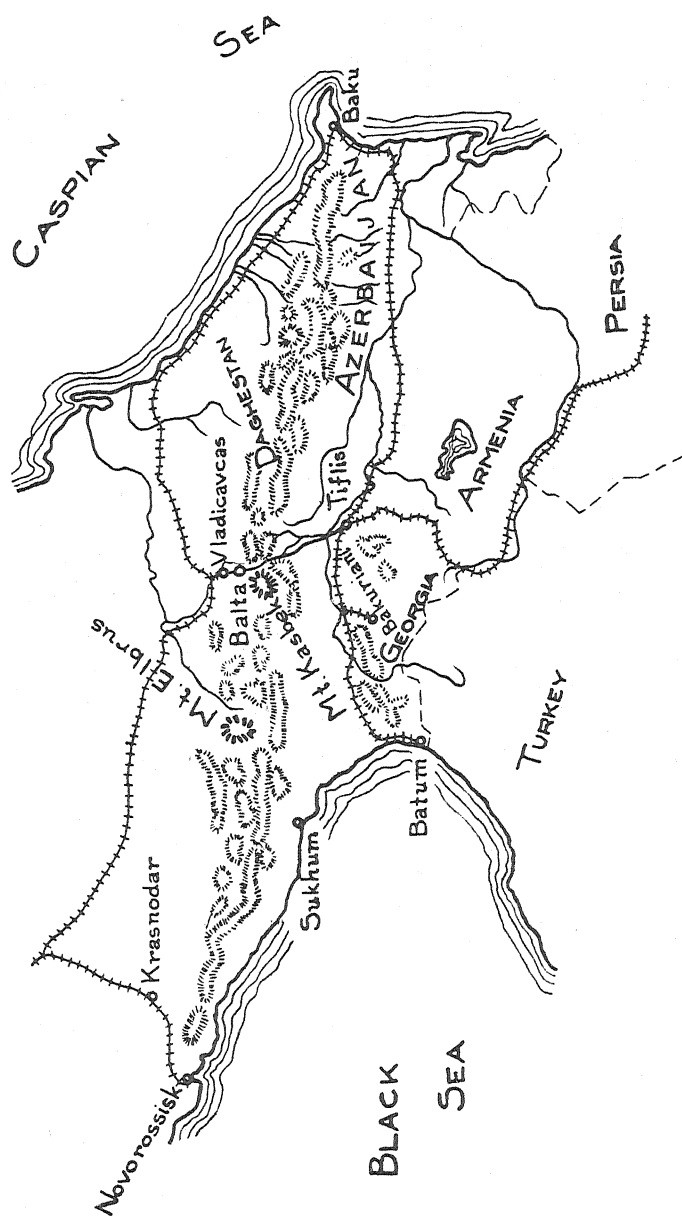


Fig. 1. The Caucasus and Transcaucasia.

strictly on the road, as the title of this paper suggests, an account of the plant life would be considerably less extensive than that given here, since the road, for a large part of its length from Vladicavcas to the divide, follows close to the base of high rocky cliffs which are all but devoid of vegetation. Side excursions are therefore necessary if one is to obtain a true impression of the flora of the North Caucasus. The Gvileti and Kasbek valleys offer the best opportunity for such trips. At least a day should be allowed for each, and the entire journey from Vladicavcas to Kasbek can be made more than once to advantage.

The journey here described extends from Vladicavcas to the divide, which is the North Caucasus part of the route. It is well first to make the trip hurriedly, which we can do with the aid of the map (Fig. 2), in order to orient one's self in regard to the major floristic features of the road.

The Georgian Military Way, from north to south, first traverses the Vladicavcas plain, following the river Terek for 14 km. to Balta (Fig. 2). Here the foot hills rise and the first forests are met with. The wooded mountain slopes continue for some 8 km. when they are replaced by treeless hills which mount to great heights and form excellent pastures. Another 8 km. brings us to Old Lars (the places named along the Way consist of nothing more than a few huts). Here a second forest zone begins which continues several kilometres beyond new Lars to the entrance of the Daryal Canyon. The 5 km. which constitute the Canyon proper are practically devoid of vegetation except for an occasional pine on a precipitous cliff many metres overhead. The rocky walls rise almost perpendicularly to tremendous heights. The Canyon is most impressive. Once out of the Canyon one comes again to treeless areas which continue to the divide. Shortly after one emerges from the Canyon, the Gvileti valley branches off to the west extending to the glaciers of Mount Kasbek. Barely 8 km. beyond Gvileti lies the village of Kasbek, its small valley also leading westward to Mount Kasbek. Both the Gvileti and Kasbek valleys rise to subalpine pastures where flowers are profuse. To reach alpine meadows requires arduous climbing. Returning to the main road, we travel another 22 km. to the divide and here reach the maximum altitude of the Way, 2345 m. (7692 ft.). 149 km. more, down through country parched in August, brings us to Tiflis. Recapitulating in tabulated form we have:

Zone	Name	Altitude in m.	Length in km.	Type plants
I	Vladicavcas Steppe	679	14	Salix, Hippophaë
II	Lower Forest (deciduous)	820	8	Fagus, Quercus, Ulmus
III	Herbaceous Slopes	960	8	Poa, Festuca
IV	Upper Forest (mixed)	1100	6	Pinus, Crataegus
V	Daryal Canyon	1300	5	Pinus, Juniperus, Saxifraga
VI	Transition	1500	8	Populus, Phragmites, Spiraea
VII	Subalpine	1700	22	Scabiosa, Cephalaria
VIII	Alpine	2200	(along the Way) —	Betula, Rhododendron

It is my aim to describe the plant life of the eight zones which we have just hurriedly traversed, as it exists in late August. Though this description

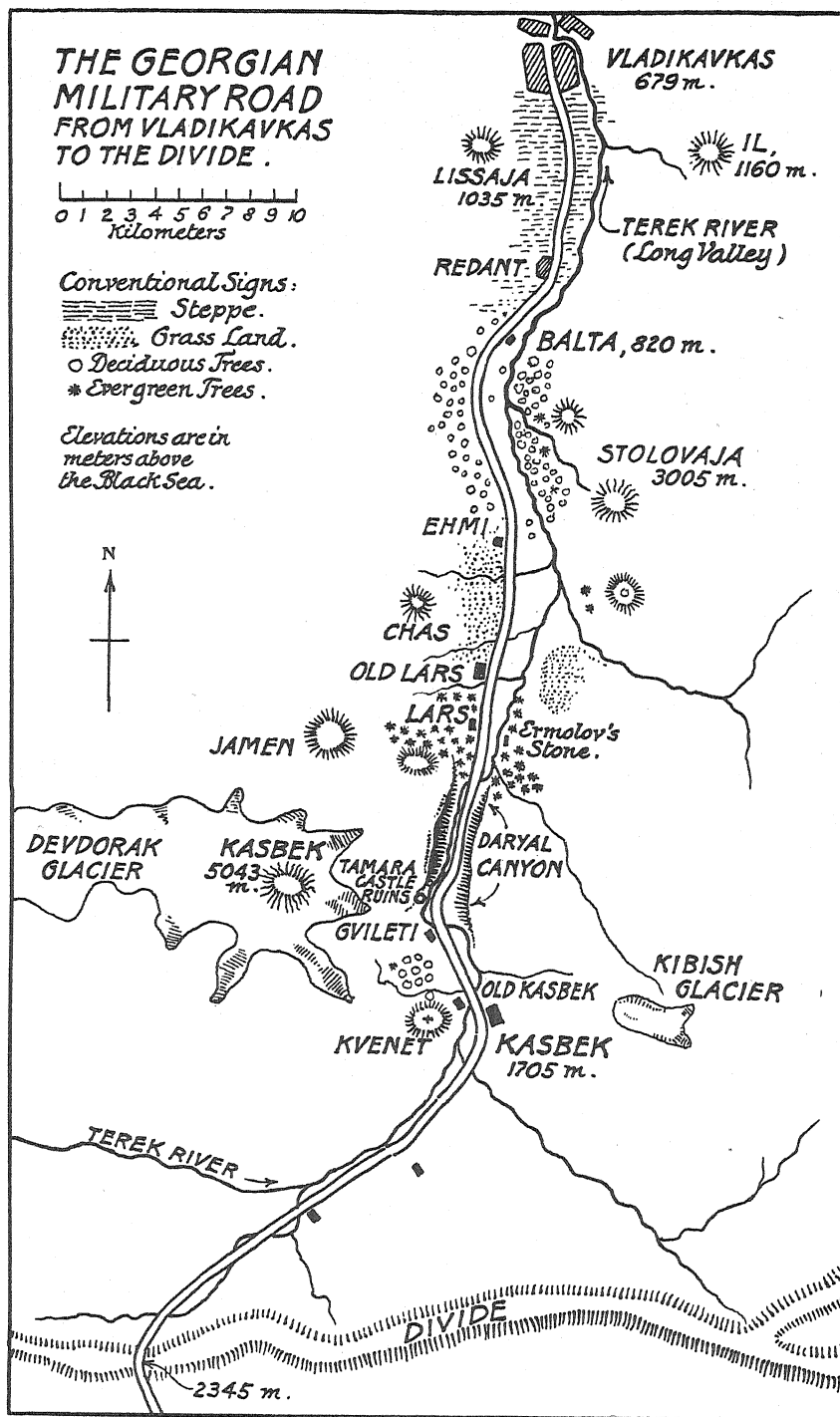


FIG. 2. Map of the northern half of the Georgian Military Way.

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of plant life in the high Caucasus is limited to the Georgian Military Way, it gives, I trust, a fair impression of the character of the North Caucasian flora in general. The third article of this series will describe the flora of the Trans- or Minor Caucasus which lie to the south.

#### ZONE I. THE VLADICAVCAS STEPPE (679 m.).

The Vladicavcas plain is watered by the river Terek whose source is the glaciers of Mount Kasbek. Much of this plain is cultivated, with the result that wild plants are few and are limited to roadsides and some few unploughed fields. The scattered trees are chiefly poplars, locusts, willows, some lindens, and wild apples. *Populus pyramidalis* is extensively planted, giving to the landscape something of the appearance of southern France. *Populus nigra* occasionally occurs. The most abundant of the trees is *Robinia pseud-acacia*, many examples of which attain great size. *Salix alba* lines the river banks from Vladicavcas into the mountains. *Pirus malus* is not infrequent. Very profuse is the European and Asian *Hippophaë rhamnoides*. It grows along the roadside as a natural hedge, though preferring the more moist river valley which it follows almost to the source. *Hippophaë* is dioecious and cauliflorous. The plant is a close relative to *Elaeagnus*, of which *E. hortensis* is also a common inhabitant of the Caucasus.

Common roadside plants in flower at this time of year on the Vladicavcas plain are *Datura stramonium*; *Cichorium intybus*, which is widely distributed, getting into the subalpine zone; and a number of showy flowers such as *Althaea* and *Lythrum*, which occur near the river but are at their best in the cooler and more moist regions within the lower mountain valleys.

#### ZONE II. LOWER FOREST (820 m.).

Balta, which consists of a single roadside house, marks the beginning of the foot hills that rise suddenly out of the plain and just as suddenly grow into the high mountains of the range. These foot hills are well forested, though chiefly with second growth. Extraordinarily abundant on the left bank is *Crataegus melanocarpa*, which forms fine well-developed trees 5 m. or more in height. With it occur *Ulmus nitens*, *Tilia caucasica* and *Salix medemi*. The willows are mostly down in the wide river bed, where they grow in great profusion. Some unusually fine old specimens of *Populus nigra* are again met with along the road. These massive trees appear to have been planted, though the species has a wide distribution throughout the Caucasus.

The woods on the right river bank are less disturbed by man and consequently are made up of larger trees, chiefly *Quercus iberica*, *Ulmus nitens* and *Fagus orientalis*. Radde<sup>1</sup> uses the specific name *F. silvatica* for the Caucasian beech. There is but the one form and it is more generally known

<sup>1</sup> Radde, G. *Pflanzenverbreitung in den Kaukasusländern (Die Vegetation der Erde III)*, Leipzig, 1899.

as *F. orientalis*. The difficulties which arose over this species in the Crimea<sup>1</sup>, where the beech resembles both *F. orientalis* of the Caucasus and the European *F. silvatica*, were circumvented by the new name *F. taurica*.

Few pines are to be seen in the lower deciduous forests. *Hippophaë rhamnoides* continues in abundance. The sharp-leaved scrambler *Asparagus verticillatus* often fills a *Crataegus* tree. Another attractive climber is *Physalis alkekengi* with its red balloons containing edible seeds.

Showy plants are numerous within the cool, shaded confines of the narrow river valley. Throughout this first wooded zone, as also in the second farther on, one meets with a wealth of flowers. *Althaea ficifolia* forms gorgeous displays of its large brilliant yellow blossoms; *A. rosea* also occurs. Another yellow flower is that of the composite *Inula helenium*.

#### ZONE III. HERBACEOUS SLOPES (960 m.).

On emerging from the forested river valley of the foot hills, one enters into more open country surrounded by high treeless mountains, which present a striking picture in their nakedness and massiveness. These subalpine fields extend for many kilometres around, high up mountain sides, and over small plateaux. A number of the bald mountains are perfect cones. The fields, often steppe-like in character, are well covered with grasses which are mostly *Poa*, *Festuca* and *Bromus* species. It is the belief among botanists that these extensive treeless mountain slopes were all forested some 500 to 600 years ago.

#### ZONE IV. UPPER FOREST (1100 m.).

The region into which we next enter, some 30 km. from Vladicavcas, is again a forested one. This second forest zone is not more than 5 km. in length, and leads directly to the entrance of the Daryal Canyon. The station Lars is about midway in this zone.

The trees are the same as those already met with. *Crataegus melanocarpa* is still very abundant, forming small pure stands and exhibiting some fine individual specimens. The deciduous trees, oak, beech, elm, linden and willow, still continue, but the character of this upper forest is marked by the pine, which predominates throughout, especially on the rocky slopes of the right river bank.

The pines of the Georgian Military Way differ considerably in form on the two slopes, so much so that from a distance one would say the tall well-formed tree of the right bank is *Pinus silvestris*, and the low scrubby one of the left bank, *P. montana*. This distinction has been taxonomically recognised, though both forms are generally regarded as of the same species, but whether *Pinus silvestris* var. *hamata*, or *P. hamata* is yet unsettled. The botanists of the south Caucasus regard *P. hamata* as the pine of all the Caucasus, with only one other nearby species, *P. armena*, which is limited to

<sup>1</sup> Seifriz, W. "The Altitudinal Distribution of Plants on the Crimean Mountains," *ante*, p. 369.



Turkey. The *montana* form of the pine along the Georgian Military Way has been recognised by Fomin and Radde<sup>1</sup> as *P. silvestris* var. *alpina*. The distinction, though taxonomically doubtful, is stamped ecologically by soil preference; the *montana* form occurs on granite.

The only other conifers along the Georgian Military Way are three junipers and a *Taxus*. Here, in the second forest zone (Zone IV), *Juniperus oblonga* occurs as a shrub, with *Taxus baccata*. We shall meet with another juniper higher up.

*Picea*, so typical of the Minor (South) Caucasus, where it forms beautiful specimens in extensive forests, is restricted to the western parts of the High Caucasus, both in the north and the south, Tiflis being the eastern limit. There is no spruce on the Georgian Military Way.

Flowers continue to flourish in small open areas. In the wet soil along the road the rich purple spike of *Lythrum salicaria* var. *intermedia* stands in great numbers. Radde cites *L. hyssopifolia* as occurring in the Caucasus, though I did not meet with it. Another blue spike is that of *Salvia nemorosa*. *Campanula rapunculoides*, *Picris strigosa* and *Aster ibericus* are pretty additions to the roadside flowers.

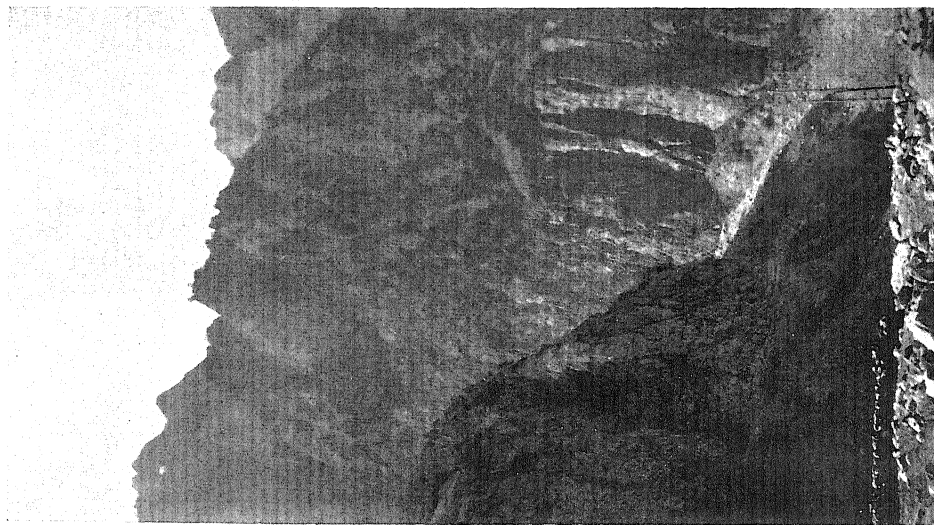
#### ZONE V. THE DARYAL CANYON (1300 m.).

The Daryal Canyon offers little encouragement to plants (Pl. XVIII, Phot. 1). In its most precipitous parts its width is barely more than that of the road and the narrow river bed combined. Its walls rise almost perpendicularly to tremendous heights. The sun enters for but a few hours each day. Yet, in its more open parts, especially near the upper end, some plants manage to exist on the rocky ledges. The *montana* form of the pine is to be seen perched high on rocky crags (Pl. XVIII, Phot. 3). Where a little soil has gathered, clumps of *Juniperus sabina* and *J. oblonga* find a foothold, so also *Berberis georgica* and *Euphorbia*. *Sempervivum caucasicum* flourishes well, tightly rooted in rock crevices, as is the habit of this genus. Here we also find a species of *Scabiosa*, the small *S. bipinnata*, and *Pyrethrum*, a less familiar genus among the asters, which occurs as the delightfully jaunty *P. parthenifolium*, clinging high where the precipitous cliffs of the Canyon open up into the sunshine (Pl. XX, Phot. 6). We shall meet with the more abundant *P. niveum* later. A third species, *P. macrophyllum*, occurs in the Minor Caucasus. Here, at the south end of the Canyon, I collected the first fern, an *Asplenium trichomanes*.

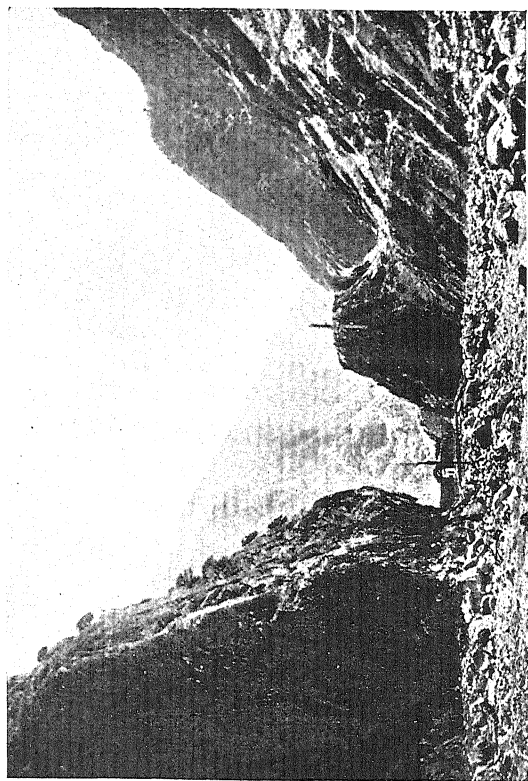
But three mosses were collected from the rocky cliffs along the road coming out of the Canyon. These have been kindly identified for me by Mr R. S. Williams of the New York Botanical Gardens; they are *Mielichhoferia nitida*, *Dicranum bonjeani* and *Sphagnum capillaceum*. The first is an old world moss and the two latter are familiar North American species.

The mammoth truncated cone of rock, which is crowned by the ruins of

<sup>1</sup> Radde, G. *Pflanzenverbreitung in den Kaukasusländern (Die Vegetation der Erde III)*. Leipzig, 1899.



Phot. 3. Open regions of Daryal Canyon with  
*montana* form of *Pinus hamata*.



Phot. 1. Upper end of Daryal Canyon, with Castle of Tamara.



Phot. 2. *Juniperus oblonga* at Gvileti.

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an ancient castle accredited to the legendary Queen Tamara, marks the upper (southern) limit of the Daryal Canyon and the beginning of the sixth (second herbaceous) zone.

#### ZONE VI. TRANSITION (1500 m.).

The Castle of Tamara stands like a sentinel before the southern entrance of the Daryal Canyon (Pl. XVIII, Phot. 1). Its position was undoubtedly selected because of strategic advantages. From this point on, the Georgian Military Way passes through high open treeless valleys, where the meadows though small are luxuriant with flowers. Herein lies the chief difference between the first and this, the second, herbaceous zone; the former has much of the steppe in its make-up, the fields are extensive, and the vegetation is chiefly grass, but in the second herbaceous zone of the upper mountain regions the meadows are small and covered with subalpine flowers.

Shortly beyond the upper end of the Daryal Canyon is the village, if such it may be called, of Gvileti. The altitude is 1500 m. To the west lies a valley which leads to the north-east glacier of Mount Kasbek. The surrounding country is very picturesque and constitutes one of the richest collecting grounds in this part of the Caucasus. At least two days should be spent at Gvileti; one may spend the night at the primitive hostelry.

Eight kilometres beyond Gvileti, at an altitude of 1705 m., lies the village of Kasbek. It is a mountain settlement of considerable size with a magnificent view of Mount Kasbek whose glistening dome rises to a height of 5043 m. (16,547 ft.). The older settlement at Kasbek is a primitive but unique little village. The valley is small and offers little opportunity for agriculture, but the natives manage to raise some wheat and cattle. The valley leads to the eastern glacier of Mount Kasbek.

The fields at Gvileti are uncultivated and therefore little disturbed by man. A mountain lake there adds an interesting plant to the flora, *Phragmites communis*, which grows profusely (Pl. XIX, Phot. 4). Small compact mounds of *Juniperus oblonga* are scattered about over the rocky floor (Pl. XVIII, Phot. 2). *Spiraea hypericifolia* var. *subalpina* grows abundantly on the cliffs, and with it *Allium ruprechtii*.

The fields at Gvileti and Kasbek (1500-1700 m.) constitute the limited region of our sixth zone. At Gvileti, the ground is mostly rock, with some grass, scattered prostrate junipers, and an occasional *Centaurea*. At Kasbek, subalpine flowers creep down into the grassy meadows between the cultivated fields. Here occur small woods of *Populus tremula* (Pl. XIX, Phot. 5). The poplars are relics of a former extensive forest and still exist because they have enjoyed the protection of the church.

The sixth zone is a transitional one, joining the lower rocky slopes to the higher subalpine fields. It is a zone characterised more by its geologic features than its sparse floristic ones.

## ZONE VII. SUBALPINE (1700 m.).

Above Gvileti lies a subalpine region of great interest and beauty (1700–2200 m.). Small trees, chief among which is the birch, alternate with flower-covered meadows bounded above by *Rhododendron* and alpine pastures.

At Gvileti, *Betula raddeana* climbs to 2400 m. and gets down to 1700 m., occurring, therefore, in both the alpine and subalpine regions (Pl. XX, Phot. 7). The more typical birch of the alpine zone is *Betula pubescens*. I am not quite certain in regard to a third kind of birch, *B. pubescens* var. *raddeana*, occurring at Gvileti. It appears to differ from both the *pubescens* and *raddeana* species and therefore was identified as a third form, though it may be identical with one or the other of the two species after which it is named.

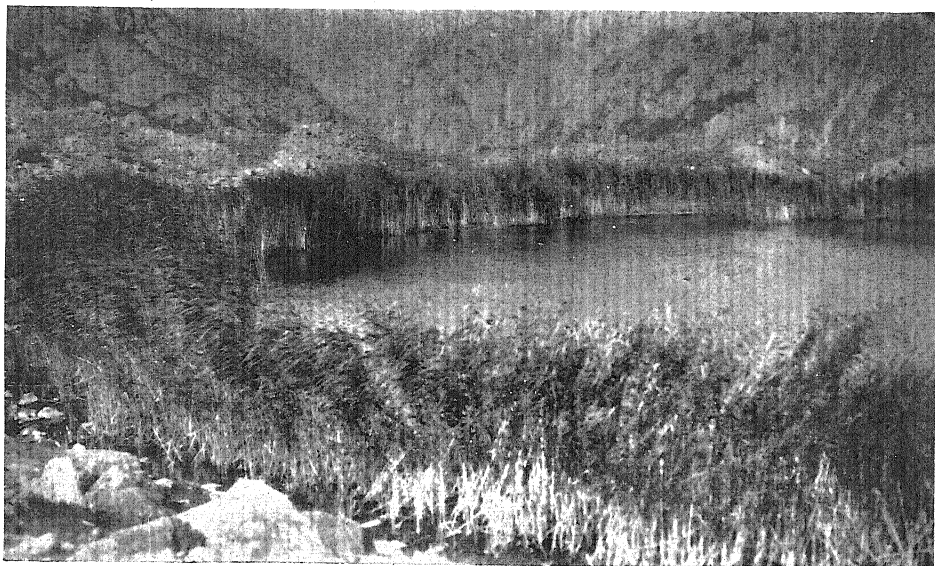
An interesting tree, of which I saw only one specimen in these higher mountain valleys, is the maple, *Acer trautvetteri*, which was growing at 2000 m. Radde says that this species may reach the tree line. Here at Gvileti it is near the tree line, but I never found it there in the Minor Caucasus, where it is very abundant, occurring just below the open subalpine woods of birch.

*Sorbus aucuparia* begins to make its appearance at 1600 m., getting up into the alpine region at 2400 m. (Pl. XX, Phot. 7). This small tree is of very wide distribution in the mountains of the Soviet Union from the Crimea to Eastern Turkestan. It is a companion to the birch. Whether to regard the two as alpine or subalpine is purely a matter of defining the limits of these zones in that particular region where we happen to be at the time. In the Crimea, neither of these two high altitude trees plays a prominent part in the plant life of the mountains, they occur only sparingly, while in the Minor (South) Caucasus (Bakuriani) they grow in great abundance, form the tree line, and on certain slopes occur at high altitudes to the exclusion of all other arboreal forms. Usually, the tree line of birch and *Sorbus* makes a convenient upper limit of the subalpine zone, but where meadows of tall, showy, subalpine plants, such as *Scabiosa*, *Delphinium*, *Cephalaria* and *Epilobium*, grow above the birches, then, naturally, we cannot regard the latter as delimiting the alpine and subalpine flora; furthermore, where the birches get so far above the fields of herbaceous succulents as to mingle with *Rhododendron*, as here at Gvileti, they become alpine, for their associates are not only *Rhododendron* but such other truly alpine forms as *Antennaria* and *Sibbaldia*.

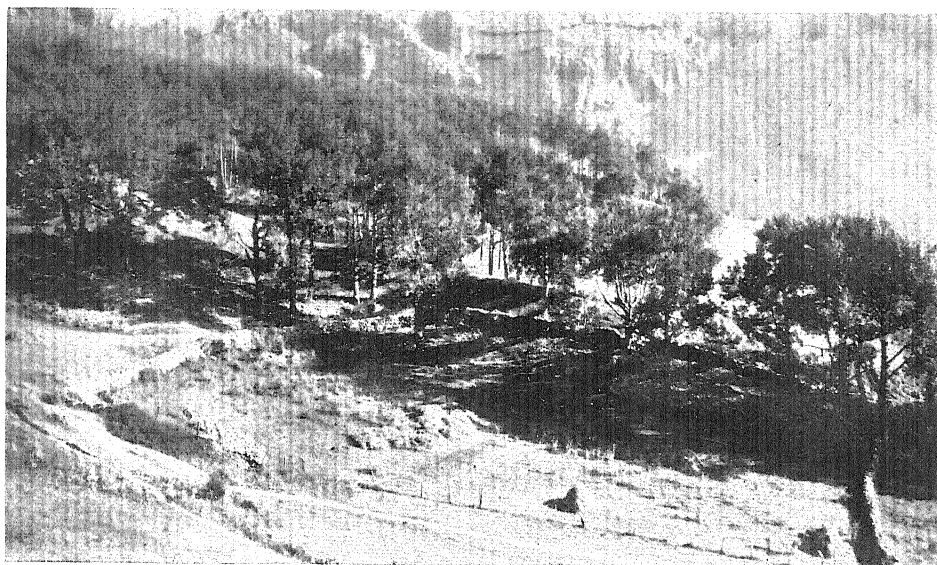
One other tree occurring here at 2000 m., though not abundantly, is *Salix caucasica*.

The trail at Gvileti, with Mount Kasbek and its glacier constantly in view, rises but little above 2000 m. before it descends again to go into the rocky gorge at the head of which is the terminus of the glacier. The trail reaches its highest point in a field of flowers of great luxuriance and beauty. This subalpine meadow extends from 2000 to 2200 m., and is almost entirely covered with a tall rank growth of herbaceous plants: very little grass is visible, and





Phot. 4. *Phragmites communis* at Gvileti.

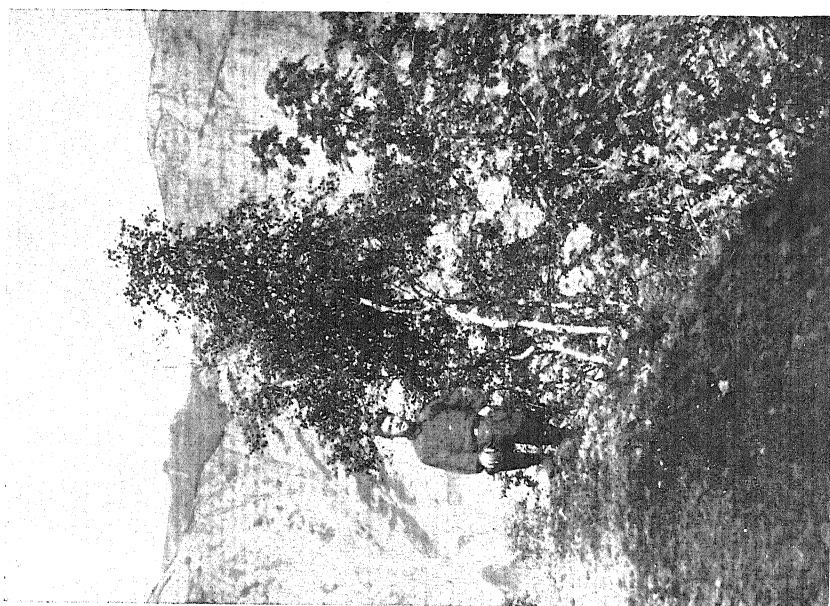


Phot. 5. *Populus tremula* at Kasbek.

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Phot. 7. *Betula raddeana* and *Sorbus aucuparia* at 2400 metres.



Phot. 6. *Pyrethrum parthenifolium* at Gvileti.

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this emphasises Timofeev's contention for the Minor Caucasus, that alpine regions contain thirty to forty, and subalpine seventy to eighty, species of herbs as compared with eight of grasses.

The plants of the Gvileti and Kasbek valleys are so much alike that it will give a more unified picture to list them together. The following are the species collected in these two localities at the beginning of August. The final identification of them has rested with Mr Dmitri Sosnovsky, of the Tiflis Botanic Garden, to whom my thanks are due.

- |                                    |                                    |
|------------------------------------|------------------------------------|
| POLYPODIACEAE                      | CISTACEAE                          |
| Asplenium trichomanes              | Helianthemum chamaecistus          |
| Athyrium alpestre                  | THYMELAEACEAE                      |
| Cryptogramme crispa                | Daphne glomerata                   |
| Dryopteris oreades                 | ONAGRACEAE                         |
| Dryopteris robertiana              | Chamaenerium palustre              |
| Polypodium vulgare var. rotundatum | Epilobium algidum                  |
| Woodsia fragilis                   | Epilobium nervosum                 |
| ORCHIDACEAE                        | UMBELLIFERAE                       |
| Gymnadenia conopea                 | Astrantia biebersteini             |
| SALICACEAE                         | Astrantia maxima                   |
| Populus tremula                    | ERICACEAE                          |
| POLYGONACEAE                       | Vaccinium vitis idaea              |
| Oxyria digyna                      | OLEACEAE                           |
| Rumex alpinus                      | Ligustrum alatum                   |
| CHENOPODIACEAE                     | GENTIANACEAE                       |
| Chenopodium foliosum               | Gentiana asclepiadea               |
| CARYOPHYLLACEAE                    | Gentiana caucasica                 |
| Alsine imbricata                   | Gentiana septemfida                |
| Dianthus alpinus                   | LABIATAE                           |
| Dianthus petraeus                  | Betonica grandiflora               |
| Minuartia imbricata                | Mentha silvestris                  |
| RANUNCULACEAE                      | Thymus serpyllum                   |
| Aconitum caucasicum                | SOLANACEAE                         |
| Aconitum nasutum                   | Physalis alkekengi                 |
| Aconitum orientale                 | SCROPHULARIACEAE                   |
| Delphinium flexuosum               | Rhynchochorys orientalis           |
| Ranunculus boissieri               | Verbascum orientale                |
| PAPAVERACEAE                       | DIPSACACEAE                        |
| Papaver bipinnatum                 | Cephalaria procera                 |
| CRUCIFERAE                         | Scabiosa caucasica                 |
| Thlaspi arvense                    | CAMPANULACEAE                      |
| CRASSULACEAE                       | Campanula collina                  |
| Sedum oppositifolium               | Campanula rapunculoides            |
| Sempervivum caucasicum             | Podanthum amplexicauli             |
| SAXIFRAGACEAE                      | COMPOSITAE                         |
| Parnassia palustris                | Centaurea fischeri var. ochroleuca |
| ROSACEAE                           | Centaurea phrygia                  |
| Alchemilla pubescens               | Doronicum macrophyllum             |
| Alchemilla tredecimloba            | Inula glandulosa                   |
| Fragaria elatior                   | Inula helenium                     |
| Rosa dumetorum                     | Leontodon hispidus                 |
| Rubus idaeus                       | Mulgedium racemosum                |
| Rubus saxatilis                    | Pyrethrum niveum                   |
| LEGUMINOSAE                        | Pyrethrum parthenifolium           |
| Medicago glutinosa                 | Senecio candolleanus               |
| Vicia alpestris                    | Senecio nemorensis                 |
| GERANIACEAE                        | Solidago virga aurea               |
| Geranium pyrenaicum                | Swertia iberica v. alleida         |
|                                    | Tanacetum vulgare                  |
|                                    | Tragopogon reticulatus             |

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The most beautiful of the blossoms is *Scabiosa caucasica*, the queen of all the Caucasian flowers.

#### ZONE VIII. ALPINE (2200 m.).

At 2200-2400 m., in the Gvileti valley, clinging to the precipitous north slopes of the mountain, grows a dense thicket of *Rhododendron caucasicum*. Intermixed with it are *Vaccinium vitis idaea*, *Sorbus aucuparia* and *Betula pubescens*. The birch, in places, occupies the ground alone. An occasional inhabitant of these higher slopes is, again, *Salix caucasica*.

The Georgian Military Way leads on from Kasbek to Kobi and to the Divide. The latter is a treeless pasture covered with grasses and the poisonous *Veratrum album*. The Caucasian lily, *Lilium monadelphum*, is also present.

From its maximum altitude of 2345 m. (7692 ft.) the Way winds down through country less magnificent than the north slopes of the Caucasus, becoming more and more arid until the semi-desert plains of Tiflis are reached at an altitude of 400 m.

## THE FENLANDS OF LOUGH NEAGH

By JAMES SMALL.

*(With a Sketch-map in the Text.)*

THE actual recognition around Lough Neagh of fenlands, as distinct from the very prevalent acid moors of Ireland, was made by the writer in June, 1928, after carrying out determinations of the hydrion concentration of the water in various drains and, as a result, comparing the flora of East Anglia with that of the Moss Lane region as listed by Miss Mary Duff, to whom the chief credit of the discovery must be given. The much regretted death of this enthusiastic field worker has delayed the detailed investigation of regions other than Moss Lane, but the closer survey of selected areas is proceeding and it is hoped to publish the data later.

### TOPOGRAPHY.

Lough Neagh is the largest inland lake in the British Isles, a sheet of water roughly 24 km. (15 miles) from north to south and with an average width of about 16 km. (10 miles). Draining the basaltic plateau of Co. Antrim, the streams of Six Mile Water and Maine River flow in at the north-east; while from the Mourne mountains comes the River Bann in the south; from the higher lands of Tyrone and Armagh comes the Blackwater at the south-west; and from the Sperrin mountains of Tyrone the Ballinderry River on the west (this must not be confused with the townland of Ballinderry in the Moss Lane region). In addition the Lough receives the waters of numerous smaller streams. The outflow occurs at Toomebridge where the Lower Bann begins to fall its 15.8 m. (51.9 ft.) into the sea some 48 km. (30 miles) away.

The average rainfall of the drainage area is approximately 76 cm. (30 in.), decreasing generally from west to east. This, combined with the slow flow of the Lower Bann, produces extensive winter flooding. The lough side is therefore rather difficult of access except during the summer months, actual fen areas being under 30 to 90 cm. of water from October to March each year. The detailed survey of such areas can proceed only slowly as local workers become available, and the present short note is given merely to indicate the presence of the fen formation in Ireland. The map illustrates the relatively small areas which have been examined in detail and the relatively large areas which in reconnaissance have been distinguished as either true fen, or mixed fen and acid moor alternating, according to slight differences in the usual limits of winter flooding and with the extensive peat cutting which may reduce the level to the critical depth for fen or even expose the underlying still relatively



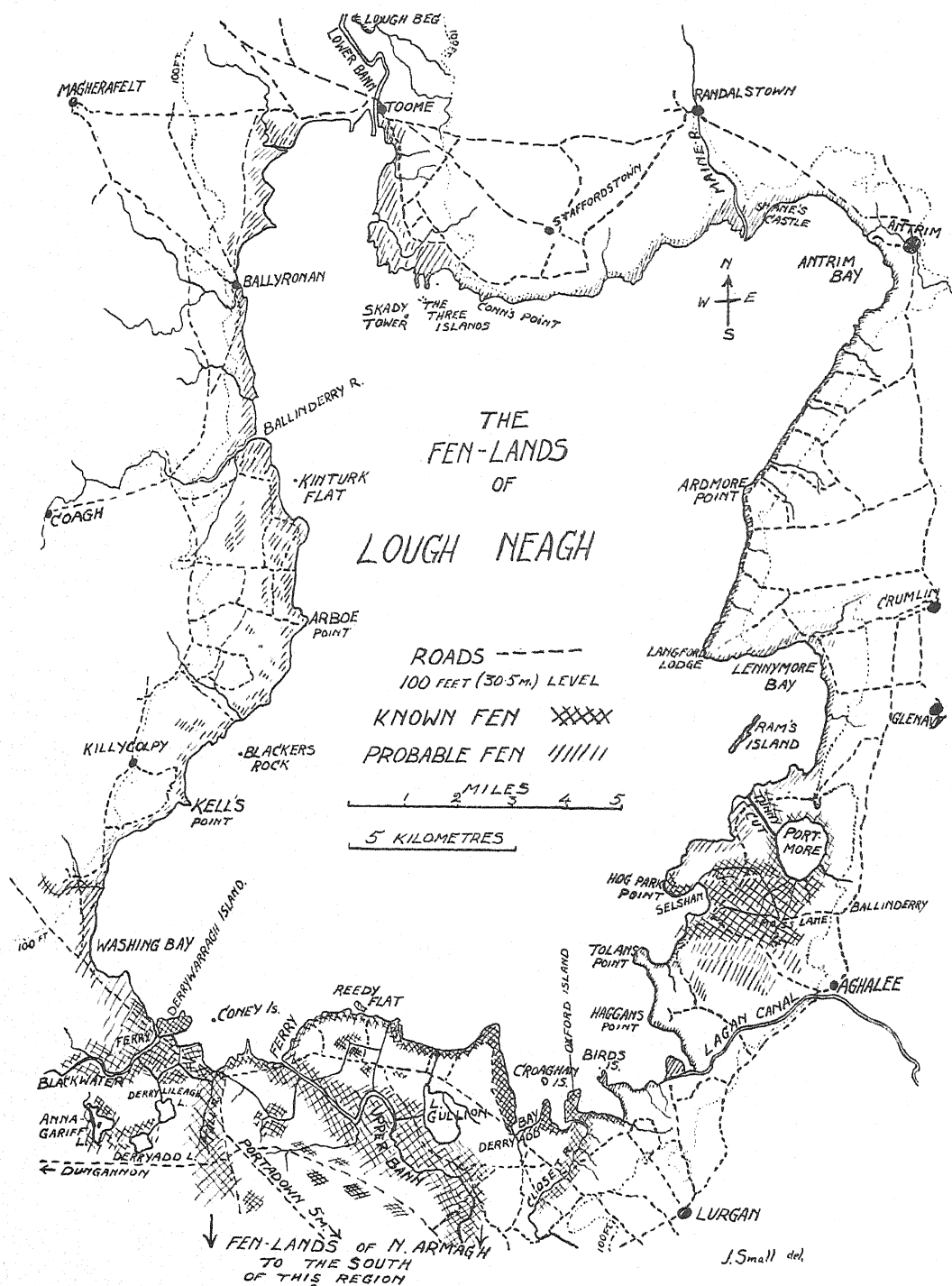


FIG. 1. Distribution of Fenlands round Lough Neagh.

alkaline marsh or fen peat. Miss J. M. White in a forthcoming publication on "Re-colonisation after peat-cutting" deals with these points in detail.

Portmore, which is connected with Lough Neagh by the Tunney Cut in summer and by several flooded areas in winter, is a typical young "broad." The water is only about 1 m. deep in summer, the substratum a deep rich black mud; the aquatic associations pass into closed reed swamp, and thence to swamp carr.

#### LOUGH NEAGH WATER.

There is no direct analysis available of the water in the Lough, but Lurgan is said to draw its main water supply from the Lough and the following are the "Results of chemical examination of a sample of water labelled 'Tap water from main' received from R. Pedlow, Esq., M.B., Lurgan." This analysis is by Prof. W. James Wilson, to whom the writer is indebted for other information. In parts per 100,000—total solids 14.0, total hardness 9.0, chlorine as chloride 1.60, nitrogen as nitrate 0.01, saline ammonia 0.0015, organic ammonia 0.0100, oxygen absorbed from permanganate 0.194.

The hardness 9.0 may be compared on the one hand with the Belfast Mourne supply 2.0, and on the other with 23 to 28 for the London Thames supply, and about 40 for London spring supplies. The hardness, mainly as calcium carbonate, is derived from the basalts of counties Antrim, Londonderry and Tyrone. The granitic Mourne supply is much softer and is acid in reaction.

The hydron concentration of the open water of the Lough is in the region of pH 7.0, and this increases in the drains to as much as pH 6.5–6.0, but never more. Since the waters of acid moors are usually in the region of pH 4.5–5.0, it was this relative alkalinity which led to an examination of the flora as possibly belonging to the fen formation.

#### FLOOD LEVELS.

The average winter rise in the Norfolk fen waters is only a few centimetres or inches, but the average winter rise in the level of Lough Neagh is about 1 m. (3 to 4 ft.), occasionally 6 ft., seldom more. Much of the land around the lough on all sides except the north-eastern section is very low-lying, so that in winter one can travel extensively by boat over summer hayfields and rood-mosses.

#### LOUGH NEAGH AS A BUFFER SOLUTION.

Lakeside peat is formed by the partial decay of plants of the aquatic formation, and by the gradual raising of the soil level passes into fen peat, which supports the amphibious or non-aquatic flora included in the fen formation. The natural tendency of the fen is to lose its relatively (or actually) alkaline ground water by leaching and drainage and to pass into acid moor by the development of *Sphagnum* which hastens the acidification of the surface waters.

The growth of *Sphagnum* may be inhibited by at least two factors: (a) a low rainfall giving an insufficient water supply as in East Anglia, and (b) a plentiful supply of neutral or alkaline ground water renewed periodically. The second factor is at present active in the Lough Neagh fenlands, where the rainfall is ample for an abundant development of *Sphagnum*.

The annual floods around Lough Neagh act as a buffer solution, removing every winter from the sphere of action the excess of hydrogen-ions produced during the summer by the normal activities and normal decay of the vegetation. The buffer capacity of this very dilute solution is undoubtedly low, but the large volume (150 sq. miles) available, and the periodic renewal of supplies every winter for even 6 months at a time, make this low buffer capacity quite sufficient to keep the hydron concentration of the soil water below the critical level for the growth of *Sphagnum*.

That this buffering effect of the flood waters is essential for the maintenance of fen conditions is proved by many details of the surveyed regions. For example, where the ground level is slightly higher than the average flood level a *Molinia* transition stage is found, with occasional *Sphagnum* and small developments of *Calluna* or *Erica*, clearly incipient acid moor<sup>1</sup>. Recolonisation, after the peat of acid moor has been cut out, furnishes numerous local cases of the critical depths for the development of swamp, fen, or the various successional communities of the acid moor. These data appear in the full accounts of detailed surveys given by Miss Duff and Miss White, who have contributed so effectively to our knowledge of this interesting region.

#### THE FEN FORMATION.

Telluric neutrality or relative alkalinity combined with a large percentage of typical fen species has been proved by Miss Duff's detailed survey of the Moss Lane region (see area south-west of Portmore), and by Miss White's detailed surveys of northern Armagh at Brackagh, Derryadd, Derryvore, Derrylard, Derryinver, Derrytrasna, etc., and along the rivers Bann, Tall and Ballybay as far south as Kilmore. These areas are cross-hatched, where they occur on the map, but some are to the south and are not included. Along much of the low-lying shore of the lough the actual soil water reaction remains as yet undetermined, but certain index plants of the reed swamp and fen formations occur, e.g. *Carex pseudo-cyperus*, *Typha angustifolia*, *Sium latifolium*, *Phragmites communis*, *Phalaris arundinacea*, *Oenanthe fistulosa*, *Carex panicea*, *Orchis incarnata*, *Frangula alnus*, *Lathyrus palustris*, *Thalictrum flavum*, *Spiranthes stricta*, etc. We can, therefore, temporarily postulate

<sup>1</sup> Occurring as it does around the crown of Derryola Island which is an island only during severe winter floods, the *Molinietum* appears here to have the status of one stage in an autogenic hydrosere, the fen prisere, and not to be part of an allogenic subsere or deflected succession as suggested for Wicken Fen by Godwin and Tansley, who take *summer* water levels there, while in the Lough Neagh area it is the winter flood levels which are the dominant edaphic factor. See *The Vegetation of Wicken Fen*, by H. Godwin and A. G. Tansley. Cambridge, 1929.

the presence of fenlands in the areas which are single-hatched on the map. The real extent and distribution of fen in these regions require detailed investigations which it is hoped will be carried out in the future.

#### COMPARISONS: EAST ANGLIA AND LOUGH NEAGH.

The following species are common to the two regions:

*Aquatic formation*: *Chara* spp., *Elodea canadensis*, *Hippuris vulgaris*, *Hydrocharis morsus-ranae*, *Lemna* 4 spp., *Myriophyllum spicatum*, *M. verticillatum*, *Potamogeton crispus*, *P. natans*, *P. lucens*, *P. perfoliatus*, *Ranunculus circinatus*, *Riccia natans*, *R. fluitans*, *Zannichellia palustris*, *Cicuta virosa*, *Iris pseudacorus*, *Mentha* spp., *Myosotis palustris*, *Nymphaea lutea*, *Ranunculus lingua*, *Scirpus lacustris*, *Sium latifolium*, *Sparganium ramosum*, *S. simplex*, *Typha angustifolia*, *Utricularia vulgaris*.

*Fen association*: *Alisma ranunculoides*, *Anagallis tenella*, *Angelica sylvestre*, *Anthoxanthum odoratum*, *Carex elata* (stricta), *C. flava*, *C. panicea*, *C. pseudo-cyperus*, *Drosera intermedia*, *Eriophorum angustifolium*, *Filipendula ulmaria*, *Galium palustre*, *Hydrocotyle vulgaris*, *Lathyrus palustris*, *Lychnis flos-cuculi*, *Lysimachia vulgaris*, *Lythrum salicaria*, *Menyanthes trifoliata*, *Myrica Gale*, *Oenanthe fistulosa*, *Orchis incarnata*, *Ophioglossum vulgatum*, *Phalaris arundinacea*, *Phragmites vulgaris*, *Potentilla erecta*, *Potentilla palustris*, *Senecio aquaticus*, *Thalictrum flavum*, *Utricularia minor*, *U. intermedia*, *Valeriana officinalis*, *Viola palustris*.

*Carr association*: *Alnus rotundifolia*, *Betula pubescens*, *Caltha palustris*, *Carex panicea*, *Cicuta virosa*, *Eriophorum angustifolium*, *Filipendula ulmaria*, *Frangula alnus*, *Fraginus excelsior*, *Iris pseudacorus*, *Ligustrum vulgare*, *Lysimachia vulgaris*, *Lythrum salicaria*, *Molinia caerulea*, *Myrica Gale*, *Osmunda regalis*, *Phalaris arundinacea*, *Phragmites vulgaris*, *Potentilla palustris*, *Quercus robur*, *Ranunculus lingua*, *Rhamnus catharticus*, *Ribes nigrum*, *R. rubrum*, *R. grossularia* (cult.), *Salix cinerea*, *Urtica dioica*, *Viburnum opulus*.

*Cladium mariscus* and *Dryopteris thelypteris* of East Anglia have been recorded from the Portmore-Selshan region but have not been found in the present survey and are commonly supposed to be extinct at these stations.

The following species occur in East Anglia but are not known from the fens of Lough Neagh:

*Aquatic formation*: *Najas marina*, *Potamogeton interruptus*, *Stratiotes aloides*, all absent from the Ulster flora; *Castalia alba* (frequent in Ulster), *Ceratophyllum aquaticum* (demersum) (rare in Ulster), *Acorus calamus* (introduced in Ulster), *Carex acutiformis* (absent from Ulster), *Carex paniculata* (local), *Rumex hydrolapathum* (local).

*Fen association*: *Calamagrostis lanceolata*, *Carex disticha*, *C. fulva*, *C. paradoxa*, *Galium uliginosum*, *Hypericum quadrangulum*, *Liparis Loeselii*, *Peucedanum palustre*, *Pyrola rotundifolia*, *Valeriana dioica*, all absent from the Ulster flora; also *Carex filiformis* (lasiocarpa), *Cladium mariscus*, *Dryopteris*

*thelypteris*, *Epipactis palustris*, *Glyceria aquatica*, *Hypericum elodes*, *Juncus obtusiflorus* (*subnodulosus*), *Oenanthe Lachenalii*, which have one or two stations in Ulster outside the Lough Neagh area.

*Carr association*: *Carex acutiformis*, absent from the Ulster flora; *Carex paniculata* and *Salix repens*, present in Ulster but not yet noted in the Lough Neagh fenlands.

*Carex hirsuta*, *Spiranthes stricta* and *Zannichellia macrostemon* are recorded from around Lough Neagh but do not occur in the corresponding floristic lists for East Anglia.

These comparisons make it quite clear that nearly all the fenland species of East Anglia which are available as constituents of the more limited flora of northern Ireland occur on one or other of the fenlands of Lough Neagh.

In conclusion the writer desires to record the sincere sorrow and great regret of himself and his colleagues that the enthusiastic worker, Miss Mary Duff, M.Sc., who made this account possible, died at an early age on October 14th, 1929.

DEPARTMENT OF BOTANY,  
QUEEN'S UNIVERSITY OF BELFAST.

NOTE. Since this account was written, records for *Cladium mariscus* in the Lough Neagh region have been found: (a) Loughgall Lake by Lloyd Praeger in *Irish Naturalist*, 1893, confirmed as still there by J. M. White, 1930; (b) Ardpatrik, Stewartstown, by T. Greer in *I.N.J.* 1930, p. 129, where *Salix repens* is also recorded from eskers at Creggan and at Lough Neagh. *Juncus obtusiflorus* has been found between Charlemont and Blackwatertown about  $7\frac{1}{2}$  miles from Lough Neagh, also *Rumex hydrolapathum* at Bannfoot on the Lough, both by J. M. White.



# SUCCESSION IN XEROPHYTIC INDIAN GRASSLANDS

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(With Plates XXI and XXII.)

THE Bombay Presidency is a long strip on the west coast of India. Excluding Sind, it measures 1100 miles in length and its average breadth is 200 miles. The Western Ghats, a mountainous range whose main ridge runs parallel to the coast, causes excessive precipitation during the monsoon on the ridge itself and creates a "rain shadow" to leeward of it. The area which we are about to describe is to leeward of the Ghats, in the neighbourhood of Poona. The rainfall occurs between June and September, the average annual rainfall being 24 in. This area is typical of a very large tract in the so-called Bombay Deccan. The cultivated crops of this tract are millets and oil seeds, while the uncultivated and uncultivable areas are covered by grasslands. The underlying rock is Deccan trap, a volcanic rock of great area and depth. It weathers into a disintegrated form called *murum* and finally produces soils of varying depth, texture and colour, mostly well drained and lacking in humus. The poorer soils have much rock still present and large boulders are common.

The long dry season at once rules out this area as a place for typical grassland in Schimper's sense. The grass vegetation is composed of (1) perennial grasses whose aerial parts wither and die (and are often burnt) annually, (2) annual grasses of varying length of life whose seed lies dormant in the ground till the next rains. Where trees are found they are mainly of the thorny types, and *Acacia arabica* is common on good soil while *Acacia leucophloea* and *Acacia catechu* are found on poor soils. These trees, however, are very much nibbled by goats and also lopped by man for firewood and get little chance to grow to any great size.

The grassland may be roughly divided into three types:

- (a) that occurring on hilly areas with scattered surface stones;
- (b) that occurring on fairly deep rich soils with a comparatively high water content;
- (c) that occurring on flat, shallow, poor soil.



Throughout all of these, species of *Aristida* and the speargrass, *Andropogon contortus*, are found, but in the hilly area xerophytic tussock grasses occur and in the low-lying areas occasionally tufts of mesophytic perennial grasses are present. The dominating factor is cattle. The village cattle are let loose every morning to roam over these lands, on which there are no fences of any kind. They begin to graze as soon as there is the faintest appearance of a green leaf and they continue throughout the year as long as there is anything left which is eatable. The cattle range freely and so affect a very wide area. Their trampling as well as their grazing has a considerable effect. At no time of the year, therefore, is there any tall stand of grass, since it is perpetually cropped level with the ground. In the hot weather, March to May, accidental fires generally sweep over the area, leaving it with a burnt surface. Ants collect the seeds of grasses and bury them in their holes, making occasionally aggregations of grass species. The stones which occur particularly on the hilly area give a certain amount of protection to the grasses growing amongst them, and also act as a kind of mulch (Plate XXI, Phot. 1). It will also be understood that this Deccan grassland is peculiarly subject to erosion which may, in the case of a hillside, rapidly remove the surface and get down to bare rock, and in the case of deep soil may excavate an ever-growing ravine. A retrograde succession is thus easily observable anywhere.

In favourable conditions the succession from rock to grassland has been studied by us in an area of 7 acres fenced in 1920 and kept under study till 1930. The succession observed was as follows:

In the hilly area the gradually accumulating soil carried first of all species of the Commelinaceae such as *Cyanotis fasciculata*. Then came the short-lived dwarf grasses *Oropetium Thomaeum*, *Tripogon Roxburghianus* and *Gracilea Royleana*. The next stage was the establishment of *Aristida funiculata* and *A. redacta* along with the annual form of *Andropogon contortus*. The unclosed land never got beyond this stage. Under enclosure the next stage was the growth of *Andropogon monticola* and *Ischaemum laxum*; *Andropogon triticeus* also occurred sparingly. In the flat shallow soil even under enclosure the tussock grasses developed very slowly unless artificially transplanted. The stage *Aristida-Andropogon contortus*, therefore, appears to be the climax of the flat, shallow area. In the deeper soils, with more soil moisture, perennial grasses appeared, but they were different from those found on the stony hill slopes. These perennial grasses were *Andropogon annulatus*, *Andropogon caricosus* and *Iseilema laxum* (Plate XXI, Phot. 2). This association was distinctly unstable, and excessive moisture caused a development of Cyperaceae, species of *Eriocaulon* and other swamp weeds, while artificial drainage brought on an invasion of the perennial grasses from the hilly area and even signs of the *Aristida-Andropogon* stage. Soil moisture determination from the three typical areas—namely, hilly, flat, shallow soil and good, deep soil—showed characteristic differences.

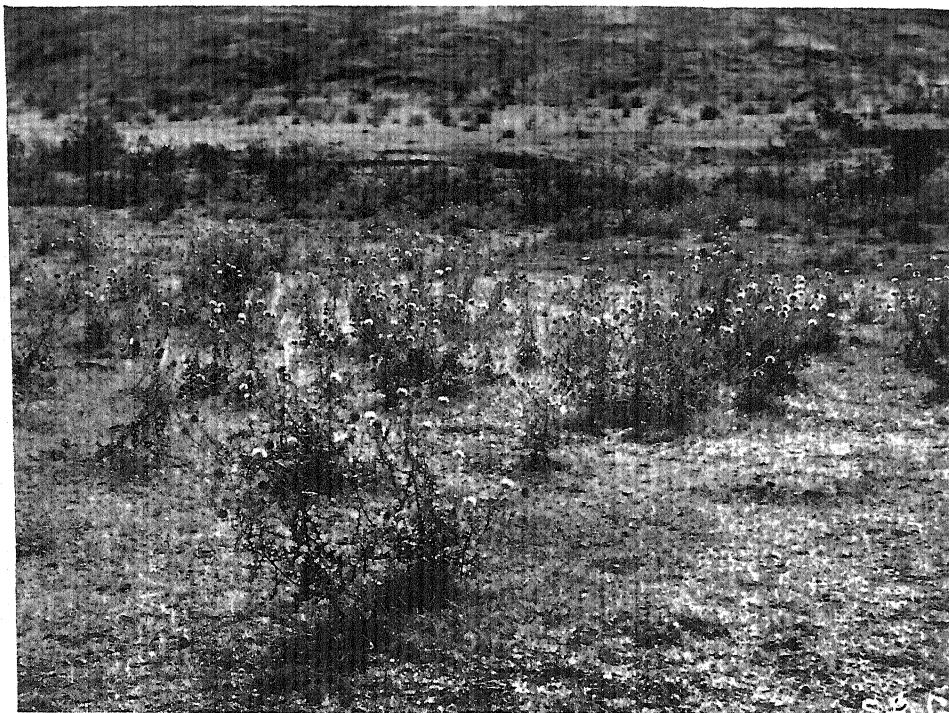


Phot. 1. Stony grassland after a fire. On the left skyline a clump of *Opuntia elatior*; on the right, *Acacia arabica*.

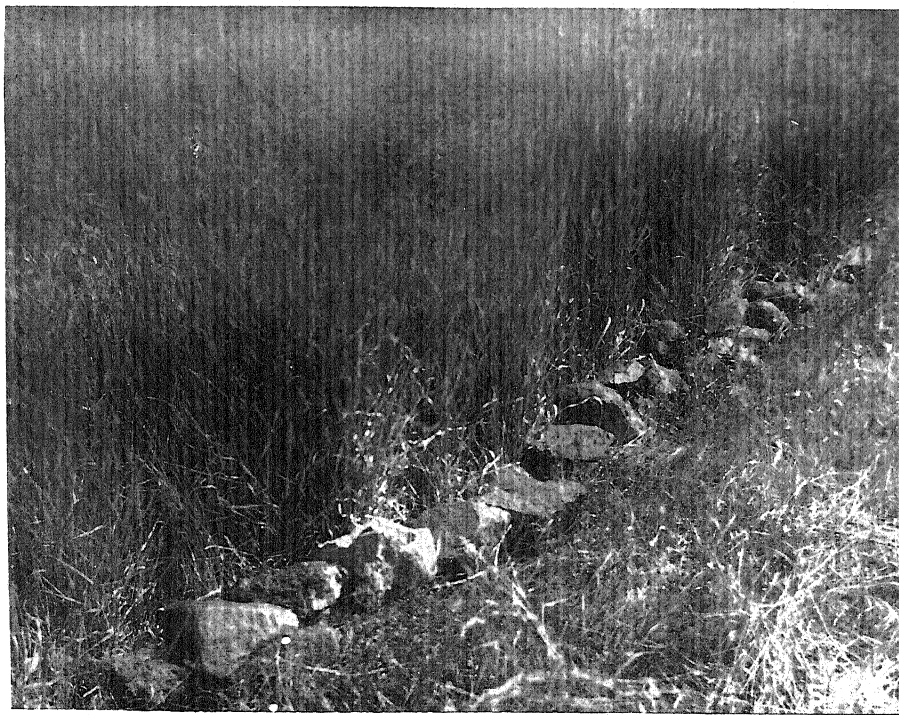


Phot. 2. Tussock grass developing in a low-lying area of good soil.

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Phot. 3. *Echinops echinatus* on an over-grazed area.



Phot. 4. Low stone embankment causing development of tussock grass.

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In the hot weather (i.e. the driest season of the year) the hilly soil had from 4 to 6 per cent. total moisture, the flat, shallow soil from 3 to 5 per cent. and the good, deep soil 15 per cent.

One unexpected result appeared from our experiment. In certain portions of the land we left the grass uncut with the idea of allowing it to rot and so add humus to the soil; the grass, however, was so fibrous that it did not decay but lay on the ground acting as a denuding agent, effectively killing vegetation, preventing germination of seeds and keeping the rains from reaching the soil. The areas which had been denuded in this manner by the overlying debris were in the following season invaded by ruderals such as *Vicoa auriculata*. It will be seen, therefore, that the grass produced must either be cut, grazed (but not over-grazed) or burnt if it is not to form an obstacle to next year's growth. Over-grazing also caused an increase of ruderals such as *Lepidagathis cristata* and *Echinops echinatus* (Plate XXII, Phot. 3).

Amelioration of such areas is distinctly possible, as we have proved by experiment. The first essential is fencing, so that the free movement and indiscriminate grazing of cattle may be checked. Low embankments of local stone along the contours check run-off, allow accumulation of silt and form starting places for tussock grasses (Plate XXII, Phot. 4). Thereafter some simple system of rotational grazing or cutting is all that is needed. Expensive fencing is out of the question, as the present value of these lands is low. There are one or two villages which have undertaken the organised management of their grasslands (even without fencing) with excellent results, utilising watchmen to keep the cattle on particular areas. Until, however, there is some pressing economic factor causing the effective management of these waste lands to become a matter of urgency, it is not likely that there will be much change in them.

# A BOTANICAL SURVEY OF GRASSLANDS IN THE SOUTH AND EAST OF SCOTLAND

By E. WYLLIE FENTON.

(*Edinburgh and East of Scotland College of Agriculture.*)

(*With a Folding Table.*)

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## INTRODUCTION.

THE present paper is based on a survey of certain grasslands in southern and eastern Scotland made during the summer of 1929. The method of examination adopted was the grid method used by Armstrong (1). Other methods are the frequency method as used by Stapledon (23) and others, and the line method of taking readings by Raunkiaer (15). Still another way is to cut turfs and weigh the removed herbage (16), a modification of Fream's method (11). It was decided to use the grid method as it would form a basis of comparison with similar analyses by Armstrong (1) and by the writer (8).

The grid method is a modification of the quadrat method of ecologists (27). Its disadvantages are that (agriculturally) it does not directly indicate the amount of food available, and that (botanically) non-gramineous plants like Wild White Clover cover in appearance a higher proportion of ground than they actually do in comparison with grasses. All methods fall short of the ideal in that they give no indication of the nutritive quality of the herbage (6, 28). Only chemical analysis can reveal this all-important point, and seasonal fluctuations (5). For survey work the grid method is the only possible botanical method, since both the time and labour involved render the turf analysis method impracticable.

The general method adopted is first to walk across the area to be investigated, and note carefully the general type of vegetation and whether it is uniform or not. Generally two diagonals of a field or area to be examined are sufficient to indicate the general vegetation. If the ground is very uneven, it may then be necessary to traverse the field several times keeping roughly parallel to a side of the field. If assistance is available matters are greatly simplified by a second person acting as a marker and keeping one in alignment both for preliminary and subsequent detailed examination. For several years now one or more of the County Staff have been present at these investigations and rendered assistance where necessary. There is also the very important advantage of first-hand information as to soil, climate, system of farming, manurial treatment, and, most important of all, method of grazing. This preliminary survey may take a very short or a considerable time, depending on the state of the vegetation. It is very important, since it warns one what to expect when the more detailed examination commences.

After the preliminary survey one knows whether readings across two diagonals or in parallel lines will be required and also whether a large number of readings will be necessary or a few will suffice. Commencing from either a corner or some other point of the field or area under investigation, the grid is thrown several yards ahead. Where it lands a reading is taken, each species and the area of ground it covers being noted. This process is repeated across the field. If the readings are homogeneous as regards the chief species, then only a few on each diagonal may be necessary; but where there is considerable variation from reading to reading the number must be increased, sometimes very greatly. These readings are then added up for each species and divided by the total number taken, the average giving the figures for the field or area. Quite recently we submitted for statistical investigation all the figures for a field where only twelve readings were taken. The result of the investigation was that the difference in figures for the chief species was significant and the order would not be changed if corrections for experimental errors were made. As this example was taken at random it seems that the method is reliable in the hands of experienced workers.

In grassland investigations like the present one, it is impossible to separate the agricultural from the botanical side since the two constantly react on each other. As this investigation is essentially botanical, the agricultural aspects have been discussed only in so far as they influence vegetation. No typical mountain or hill grasslands are considered in this survey.

#### SHORT LEYS OR TEMPORARY GRASSLANDS.

##### *First-year grasslands.*

The botanical composition of grasslands which have been recently sown are, other things being equal, determined by the nature of the seed mixture. The other factors are soil conditions, climate, altitude, exposure,



and the treatment of the grassland, mechanical, manurial and grazing. Where the custom is to employ short leys or grassland of short duration (about three years) it is generally found that the land is in good heart and arable farming is flourishing. This necessitates as much soil under cultivation as possible, and under such conditions permanent grassland is either absent or else on the higher reaches or on unreclaimed land. It is obvious that under such conditions the various factors are generally favourable to good germination and growth and to subsequent skilful treatment. As a result, if the seed mixtures are at all similar, the grasslands will tend to show a strong similarity. The failure of any of the important clovers in the mixture, such as Red or White Clover, or the substitution of Dutch White for Wild White, would completely alter the flora of the grassland. From a practical point of view, however, the two great advantages of the short ley are that quick-growing shorter lived plants can be used and a large bulk of fodder obtained, and any weakness lasts only three years; whereas in a long ley or still more in a permanent pasture it may mean a loss over a long period, if not the breaking up of the grassland. A further point is that if breaking up is necessary and if the grassland has not been successful, the result may be adverse on the succeeding crop.

On examination of the four examples of the first-year stage of short leys, it will be seen that they show a strong resemblance. Nos. 1 and 2 show a very strong resemblance to No. 4. Wild White Clover is less plentiful and Perennial Rye Grass dominant. Being in a different district and at a higher altitude the difference in the factors is quite sufficient to account for this, as the proportion of ground covered by White Clover and Rye Grass fluctuates during the season. No. 3, however, is somewhat different. It will be seen that there is no Red Clover and only 4 per cent. of White Clover, Rye covering 66 per cent. of the ground, while 19 per cent. of the area is bare. This points to a failure of the Red Clover, and, later, of White Clover to develop. If the 19 per cent. bare space is reduced to the average figure of Nos. 1, 2 and 4, and the amount deducted added to White Clover, No. 3 shows a striking resemblance to No. 4. It is not in general safe to manœuvre with figures this way to indicate or attempt to prove what is the cause of any weakness. But in the present case, the field having been seen and experience of such work gained, the method holds good, as is indicated by reference to Nos. 5 and 12. The Red Clover was not too successful, and, following on this, the White Clover has failed to make an adequate showing. The Clover present was Wild White Clover. Wild White by spreading conserves surface moisture and prevents a high proportion of bare space (9). The slightly higher proportion of Cocksfoot is another fact which points in the same direction. A too heavy crop, or the laying of the crop, may also seriously depress the clovers. Unless Wild White Clover appears and spreads in No. 3 during the next two years, there is every probability of weeds filling up the bare areas and reducing the

value of the grassland. Another point of importance is that with so much bare space the heavy loss of moisture will seriously retard the growth of plants already present. A somewhat similar case to this is No. 25. The effect of cutting for hay is to favour the taller-growing grasses (and Red Clover if present) and to depress plants of shorter and more spreading growth. In 25 A White Clover occupies 9 per cent. of the area, while Rye accounts for 35 per cent., Cocksfoot 27 per cent., and 21 per cent. is devoid of vegetation. In 25 B, which was grazed and therefore kept short, Wild White Clover has flourished and spread, with the result that the area devoid of vegetation, in spite of a drought, is only 9 per cent. against 21 per cent. in A. On the other hand, Rye and Cocksfoot show a reduction as might be expected. The difference is even greater than the figures indicate, since there was far more food for stock in 25 B than in 25 A, which was suffering from drought and yielding very little keep. The absence of Red Clover in 25 clearly indicates the use of Broad Red in place of Late Flowering Red. It also strongly suggests the same conditions in No. 3.

*Second-year grasslands.*

In the second-year grasslands there is a natural tendency for Perennial Rye Grass to decrease and Wild White Clover to increase. Cocksfoot will probably also show a slight increase, although it is usually in later years and in long leys that Cocksfoot reaches a high figure. This is due to the fact that the typical commercial Perennial Rye is not truly perennial but dwindles to a small proportion of long-lived survivors by the third year after sowing. Another point is that Cocksfoot is a slower-growing plant in its early stages than Rye Grasses or Red Clovers, and therefore gets retarded by these till the competition from that source decreases. Timothy is also affected in a similar way. Rough Stalked Meadow Grass, on the other hand, may flourish at a much earlier stage, since it is one of those plants which do much better when growing with other plants than by itself (13 a).

Comparing the second-year grasslands examined the four examples tend to fall into two classes. The classes can be distinguished by either a high proportion of Wild White Clover and a small quantity of Rye Grass or the proportion of Rye is high and Wild White Clover less than in the former class. Nos. 5 and 6, though for different counties, show a strong resemblance, the presence of a high proportion of Yorkshire Fog in No. 5 accounting for the difference in proportion of Wild White Clover. It is of interest that No. 5 is on the same farm as No. 3 of the first-year grasslands. It indicates the probable outcome of the absence of Wild White Clover (or the use of Dutch White), an insufficient number of plants present to spread in the early stages and consequently the danger of too high a proportion of bare space. No. 6 was a fine pasture carrying a large number of stock in good condition—always a good test of the condition of the grassland. No. 7 shows a good proportion

of rye grass and a good quantity of White Clover. As No. 7 is from the same farm as No. 1, it will be seen that there is little difference in the second year except that there is an increase of bare space by 6 per cent. This may quite easily be due to harder grazing. No. 8 shows a high proportion of Rye for the second year, Meadow Grass (Rough Stalked) and Cocksfoot making a good appearance. As No. 8 is from the same farm as No. 2 it is evident that there is no marked difference during the second year beyond an increase in the grasses. Except for the large proportion of Yorkshire Fog in No. 5, the second-year grasslands show no indication of reverting to a more natural type of vegetation, largely due to the good fertility of the soil, and the grazing of the vegetation being adequate. It will also be noted that Timothy has made an appearance in measurable quantity for the first time.

#### *Third-year grasslands.*

The grasslands in the third year of growth show little change from those already examined. There is a rather natural tendency for Perennial Rye and Wild White Clover to form an association and to dominate completely the vegetation, as is true of some of our best grasslands (1, 11). In Nos. 9 and 10 the vegetation consists essentially of Wild White Clover, Rye Grass, some Cocksfoot, and a little Timothy. No. 9 is on the same farm as Nos. 1 and 7. It shows little change from the first- and second-year grasslands—some improvement, indeed, since the bare space has been considerably reduced—while apart from the presence of Field Thistles, weeds have made no progress. No. 10 shows a high proportion of ground covered by Wild White Clover, while Rye Grass (10 per cent.) and Rough Stalked Meadow Grass (12 per cent.) give a total of 22 per cent., which is quite a good proportion of nourishing grasses. A trace of Yorkshire Fog and 2 per cent. Buttercup is not a matter of serious importance. Cocksfoot with only 1 per cent. is very low, doubtless due to a light seeding.

#### *Fourth-year grasslands.*

Grasslands in the fourth year show little difference from the third year. The most noticeable change is the decrease in Perennial Rye Grass, which is replaced by Cocksfoot, Rough Stalked Meadow Grass and in one case even by Timothy. In No. 11 Yorkshire Fog, even in the fourth year, has not made great progress, although 2 per cent. is more than enough of such a grass. Other weeds are not present except an occasional plant of Field Chickweed (*Cerastium arvense* chiefly, sometimes *C. vulgatum*). The large area of ground covered by Rough Stalked Meadow Grass (25 per cent.) points to a good supply of moisture and a development of the association with Wild White Clover which has been noted elsewhere (24). No. 12 is very interesting since it is on the same farm as Nos. 3 and 5. The high proportion of Cocksfoot and Timothy (10 and 5 per cent. respectively) is important, showing that the land

is in good fertility. The high proportion of ground covered by Wild White Clover (76 per cent.) suggests that the very low percentage in No. 3 in the first year may be due to the depression of Wild White Clover in the early years. Another obvious point is that in No. 12 grazing has been confined chiefly to cattle and horses. Had sheep been grazed and the grazing close, Timothy would not be present in such quantity in the fourth year.

#### LONG LEYS AND PERMANENT GRASSLANDS.

When we pass from an examination of grassland in its fourth year to long leys and permanent pastures the differences are frequently more in degree than in actual flora. Some long leys and even some permanent grasslands show a shorter list of plants present than the typical temporary ley. The fertility of the land, the care and treatment of the pasture and the skilful control of grazing animals can readily produce this result. No. 13 is an excellent example of such a type where the grassland is 17 years old. The Wild White Clover (70 per cent.), Perennial Rye (26 per cent.) association accounted for 96 per cent. of the area. Yarrow covered 1 per cent. and the remainder consisted of traces of Meadow Grass, Cocksfoot, Field Chickweed, *Geranium*, with an occasional plant of other species. This splendid pasture, created and maintained by artificial means, is comparable with the magnificent lawns of some of the Oxford Colleges, which have been achieved by constant care and similar treatment over a long period of years. In one case the result is achieved by grazing and in the other by cutting. In both cases the vegetation has settled down to a definite association which will remain constant so long as the factors, which brought about and at present maintain them, do not vary.

Nos. 14 and 15 are from the same farm and offer an interesting comparison. The outstanding difference is that No. 14 has 32 per cent. of the ground occupied by Bent Grass and 2 per cent. bare. Wild White Clover, Perennial Rye and Rough Stalked Meadow Grass all give a good proportion, while Crested Dogtail is also present in quantity. Both contain some Yorkshire Fog. In No. 14 there may have been too much bare space in earlier years and Bent and Yorkshire Fog have occupied the vacant space. It was noticeable that the grazing of No. 14 had been quite inadequate. In No. 15 it will be seen that the higher proportion of Clover, Rye and Meadow Grasses have kept out Bent Grass, and with Crested Dogtail and a little Cocksfoot, Yarrow, Yorkshire Fog and Buttercup have left no space bare of vegetation. The presence of Crested Dogtail points to grassland of a perennial type, for in many agricultural areas the plant is indigenous to the soil. It is a matter of further interest that Nos. 14 and 15 are on the same farm as Nos. 3, 5 and 12. The series show that where the original plants succeed in occupying the ground there may be little significant change in the vegetation. Where there are unpopulated areas, Bent or Yorkshire Fog or both, with other weeds, may

not only gain access but successfully maintain themselves and perhaps spread, while bad or insufficient grazing always favours inferior plants.

No. 16 is a pasture which has been in grass for 30 years. It is grazed by cattle and sheep which receive at times a supplementary ration of cake and a small quantity of potatoes. This method of feeding stock in the field is equivalent to manurial treatment, since the extra ration is largely returned in the dung of the animals. It is customary on many of the best pastures in England. The proportion of the ground covered by the various plants present, although not approaching that of the fine English pastures examined by Armstrong (1) and Fream (11), is not dissimilar from some English pastures where Rye Grasses are not present to any extent (8). The altitude and exposure are indicated by the presence of 3 per cent. Sheep's Fescue covering, while Bent (10 per cent.) and Crested Dogstail (15 per cent.) account for a quarter of the covering vegetation. In spite of this, 60 per cent. Wild White Clover and 10 per cent. Rough Stalked Meadow Grass, covering practically three-quarters of the ground, indicate that the soil is in good condition, while the condition of the stock was conclusive proof that the nutritive value of the pasture was high. No. 17 is very interesting, as it is grassland which has never been under cultivation as far as records are available. The area lies high and is rather exposed, with plentiful rainfall and a rather poor soil, which is distinctly acid. In keeping with all semi-natural grasslands the total number of species present at the time of examination is far higher than in the artificial grasslands. Although a few isolated plants of Wild White Clover were present, no trace of Rye, Cocksfoot, Timothy or Meadow Grasses could be found. In fact, beyond Rushes and some Yorkshire Fog, Bent virtually supplied the whole of the vegetation. This is very similar to the vegetation of some of the grasslands on the fringe of Dartmoor (8). The poor quality of the grazing, the reluctance of animals to graze on such vegetation and the lateness of the growth, with soil and other factors, all tend to bring about just that condition of affairs which favours Bent Grass. Even fields which are sown down with a good seed mixture may ultimately revert to such a vegetation, where the fertility is low and where treatment and grazing are inadequate (25).

#### HAY v. GRAZING: EFFECT ON VEGETATION.

Reference has already been made to the importance of grazing. The nature and extent of grazing may have very far-reaching results on grassland (10). Similarly cutting for hay produces a totally different result to that of grazing (19). Cutting for hay may lead after several years to a very different flora, as hay means tall growth with probably two annual removals, while grazing is practically a continuous process keeping the herbage short. The only example considered is No. 25. In 25 A the grassland was cut for hay and in 25 B, which is a half of the same field, the grassland was grazed. Although at present the dividing fence has been removed and both halves are grazed



the result of the previous treatment is most striking. The flora of both A and B are the same, but the proportion of the ground covered by each species is in some cases very different. As might be expected of a hay crop, Rye and Cocksfoot being tall-growing plants and competing with Timothy, the other plants are greatly suppressed. This is particularly the case with Wild White Clover. The failure of Wild White Clover means that bottom turf is not developed and bare spaces are left. The figures clearly bring out these points. In 25 A Rye covers 35 per cent. of the ground, Cocksfoot 27 per cent., while 21 per cent. is devoid of any vegetation and only 9 per cent. is covered by Clover. In 25 B Wild White Clover occupies 50 per cent. of the area, Rye 20 per cent., and Cocksfoot 12 per cent., only 9 per cent. being bare. A point of considerable interest is that no Timothy is present in 25 B. This is due to grazing, as Timothy is much more of a hay than a grazing grass. Where sheep grazing is the rule Timothy seldom survives long because the close grazing of the sheep kills it (19). Should the pasture remain down for several years the 21 per cent. bare space of 25 A will most assuredly be invaded by Yorkshire Fog and Bent as well as by weeds. This will greatly reduce the value of the grazing, and may steadily and successfully oust the more useful grasses as well as Wild White Clover. The difference between the two halves A and B is even more marked than the figures suggest. B was much greener and the vegetation more luscious and nutritious. In A much of the vegetation was dry, wiry and unappetising, as was clearly shown by the fact that all the stock were grazing in the B half. The important point is that both A and B were 2 years ago the same, and that in such a short time different treatment should cause such a marked change, which in a few years time may lead to A becoming a poor area of almost semi-natural vegetation, while B has the possibility of developing into a really good pasture. This differentiation would be aided also by the selective grazing of the cattle and sheep, unless means are taken to counteract this natural tendency.

#### THE EFFECT OF THE STRAIN OF WHITE CLOVER ON THE VEGETATION OF GRASSLANDS.

It has been very noticeable while considering previous grasslands that Wild White Clover is one of the most important if not the most important unit in the artificial association of plants raised by the farmer. Consequently any inherent difference in Wild White Clover plants will have a very far-reaching result in the final flora of the grassland after the vegetation has settled down to a more fixed phase. The strain, or pedigree, or nationality of the seed is most important, since the plants arising from such seed vary in constitutional strength, resistance to disease, ability to compete with other plants and in persistence. As the proportions of ground held by the various species in an artificial association of plants such as one finds in a pasture are in a state of mobile equilibrium, weakness or strength in any one species imme-



diately affects the other plants, which tend either to increase or decrease as the case may be. It is not so simple as a matter of increase or decrease, since, before the others present have succeeded in establishing any change, interlopers, or plants other than those sown, may appear, and thus completely alter the centre of gravity of the balance of power between the species originally sown. Since some of these interlopers are probably indigenous to the soil or strong-growing plants which are not readily grazed and thus kept in check, the vegetation may completely alter and in a short time present a very interesting study in plant ecology. Even in the early stage such changes can be seen and the final result foreshadowed. No. 20 is a good case in point. The mixtures were sown in the same field and were different only in the strain and nationality of the White Clover. A was Dutch White, B New Zealand White, C Kent Wild White, D Polish White, E a local strain (obviously Dutch White). The figures expressing the proportion of ground covered indicate at a glance the far-reaching result of using inferior strains and nationalities. No. 20 C with Kent Wild White Clover is the best plot, clover covering 70 per cent., Rye 16.5 per cent., while no ground is devoid of vegetation. Next in order comes No. 20 B sown with New Zealand White Clover. The New Zealand White Clover was evidently a mixture of White and Wild White since it covers only 26.5 per cent. of the ground; Rye accounting for 34 per cent., Meadow Grass for 10 per cent., and Cocksfoot for 8 per cent. There is, however, 16 per cent. of the ground unoccupied, while 2 per cent. is occupied by Yorkshire Fog. Nos. 20 D and 20 E are about the same, the latter being perhaps a shade better; both have 16 per cent. of the ground bare and a considerable quantity of weeds. No. 20 A is the poorest, with 22 per cent. of the ground bare, 8 per cent. occupied by Yorkshire Fog and 2 per cent. by Bent, while weeds are plentiful. The condition of the vegetation in each of the five sections of the field was more marked even than the figures suggest. The grassland was only in its second year and the high proportion of unoccupied ground, with the considerable quantities of weeds in some of the plots, points very clearly to a herbage which in a few years will be a happy hunting-ground for botanists but of little use to a farmer. The importance of Wild White Clover for covering the bare spaces, adding nitrogen to the soil and conserving the surface moisture, is very evident in No. 20.

#### SOIL CONDITIONS AND MANURIAL TREATMENT OF GRASSLAND.

Soil conditions are of course of fundamental importance in determining the vegetation of any district. The late Robert Smith in his vegetation survey of Midlothian (21) showed this fact, which was also emphasised by the late Dr Peach (21). It was also well illustrated in Dr Crampton's researches in Caithness (4). In agricultural areas soil conditions may be greatly modified and in some cases entirely altered. This is well illustrated in the manurial treatment of old grassland. The soils of many areas of old or permanent grass-

land are frequently deficient in one or more of the vital elements of plant food—nitrogen, calcium, phosphorus and potash. Frequently it is lime or phosphates which are lacking. When such a deficiency is made good the vegetation of the treated area may completely alter, many species disappearing and others spreading, while a few not previously evident may appear. No. 21 is a very good example of the change brought about by such artificial means. In the untreated area 21 A Bent covers 62 per cent. of the ground 7.5 per cent. is bare, 2.5 per cent. is occupied by Sorrel, 5 per cent. by Yorkshire Fog, 3.5 per cent. by various weeds and only a trace by White Clover. Rye Grass, Crested Dogstail and Cocksfoot are present in small quantities. After treatment with basic slag an extraordinary change occurs, for Wild White increases from a trace to 63 per cent., Rye from 5 per cent. to 15 per cent., while Bent decreases from 63 per cent. to 12 per cent. and Yorkshire Fog from 5 per cent. to 3 per cent., there is no bare space and weeds have virtually disappeared. In fact the vegetation is comparable to some good artificial grass fields. When kainit is added as well as basic slag the change is not quite so marked (No. 21 C), indicating that the soil is not deficient in potassium. Superphosphate (No. 21 D) as well as superphosphate with kainit (No. 21 E) are about the same as 21 C. It will be noticed that some weeds are still present in 21 D and 21 E. No. 21 F shows the least improvement. This might be due to the fact that neither nitrogen nor lime was deficient, or that there is another deficiency as well as that of lime. It may be (as frequently happens) that a good application of lime in any form gives little actual improvement for some years. In fact lime at times seems at first to make matters worse than they were before the application. One point is very evident and that is a phosphate deficiency. The marked decrease in Moss and Sorrel both point to acidity and to deficiency of the soil in lime. This explains the superiority of basic slag to superphosphate, since the former contains some lime while the latter has an acid reaction. In No. 22 the grassland was very old pasture which had long ago been under the plough. It had been grazed but not to the same extent as the rotation grasslands. Bent covered 64 per cent. of the ground, Ling 10 per cent., various weeds 5 per cent., Moss 5 per cent., *Luzula* 2 per cent., and Self Heal (*Prunella*) 3 per cent. There was no trace of White Clover, but Greater Bird's Foot Trefoil (*Lotus major*) accounted for 10 per cent. of the area. The presence of Greater Bird's Foot Trefoil is typical of such semi-natural grasslands. A small strip of this grassland was treated with basic slag *plus* potash salts. The result was remarkable. Wild White Clover appeared and increased to the extraordinary proportion of 85 per cent., Bent decreased from 64 per cent. to 10 per cent., while Moss, Ling and weeds were completely crushed out. But for the absence of Rye Grass, which will almost certainly appear in the near future, the treated area compares most favourably with a good pasture field of rotation grass. The change is not due merely to the addition of phosphate and potash salts, but also to the harder grazing following on the

improved quality of the vegetation. This secondary result of manurial treatment is most important, for if grazing is inadequate improvement will not be so marked and may be only of a temporary nature.

No grassland investigation would be complete without a consideration of lime, or to put it another way, the question of acidity. In regard to 21 F it was pointed out that lime did not always give an immediate result as far as the vegetation is concerned, but there are numerous instances where the application of lime is soon reflected in the changed vegetation. No. 23 is a good example of this, although a quantity of road compost was also added at the same time. The field was a large one on the crown of a low hill about 400 ft. above the sea-level. The soil although not of a high order of fertility was by no means poor, though on the light side. Some years ago half the field was treated with lime and a compost chiefly of road scrapings. The second-year grass showed a very remarkable and clean cut difference in the vegetation and appearance between the treated and untreated portions. The untreated was at a distance a study in red and violet. On closer inspection it was thin and bare, but the extraordinary quantity of Sorrel (*Rumex acetosa*) and Wild Pansy (*Viola tricolor*) was astounding, the floral colours making the quantities seem greater than they actually were. Of the grasses Perennial Rye alone made any great showing, occupying 38 per cent. of the ground, Yorkshire Fog ranking next with 5 per cent. Alsike Clover occupied 0.5 per cent. of the ground, Greater Bird's Foot Trefoil 1 per cent., but no other legume was present. Hawkweed occupied 4 per cent. and Field Mint 3 per cent. of the area. Hence, apart from Rye Grass, the useful plants were virtually absent or present in such small quantities that they gave no value to the pasture. The treated area showed a remarkable difference, for Wild White Clover occupied 25 per cent. of the ground, Perennial Rye 55.5 per cent., Cocksfoot 4 per cent., Timothy 0.5 per cent., Alsike and Red Clover 5 per cent. each, Sorrel and other weeds had completely disappeared, while the bare area in spite of a dry summer and an exposed position was only 4 per cent. Of the inferior grasses Yorkshire Fog alone was present to the extent of 1 per cent., a very marked reduction. The vegetation of the treated portion compares very favourably with the second-year grasslands investigated and indeed shows a strong resemblance to No. 8. It is unfortunate that there is now no means of determining what mineral ingredients of the road scrapings may have played a part with the lime in improving the fertility of the soil. The finely ground particles of some road metal may release a considerable amount of plant foods such as potash, phosphates, and sometimes even lime, as has been pointed out by Hendrick and Newlands (12) for some Scottish soils. The chief item in the change is undoubtedly lime, which not only removed acidity but so improved the physical and chemical condition of the soil that Mint disappeared. The reduction of Sorrel from 13 per cent. to nil is remarkable. A good example of the influence of lime alone is shown in No. 24. The field is

at present in rotation grass and has therefore been in cultivation for some time. The untreated portion is dominated by Bent Grass (45 per cent.), with a little Yorkshire Fog (2.5 per cent.), Perennial Rye Grass (2.5 per cent.), Greater Bird's Foot Trefoil (2.5 per cent.), Sorrel (2 per cent.), and Gorse (0.5 per cent., rising to as much as 2 per cent. in some parts), but most important of all 44.5 per cent. of the ground was bare. There were traces of Cocksfoot, Crested Dogstail, Red and White Clover. On the portion treated with lime some years ago the vegetation is entirely different. Wild White Clover covers the ground to the extent of 82 per cent., Rye Grass has increased to 15 per cent., Red Clover and Cocksfoot have both increased. Yorkshire Fog shows a marked decrease, while Yellow Suckling Clover has appeared and Greater Bird's Foot Trefoil and Gorse have disappeared completely. The three outstanding points are that all bare spaces have disappeared, Sorrel can no longer be found, while Bent Grass is reduced from 45 per cent. to a few isolated plants. The treated part, 24 B, shows quite a strong resemblance to some of the short rotation grassfields of the more fertile soils. It is evident from a study of Nos. 23 and 24 that lime is the deciding factor in both cases, and that acidity leads not merely to the presence of Sorrel and weeds but to a condition of affairs where Creeping Bent obtains a position of complete dominance. This is clearly shown in No. 17 which is practically the neighbouring field to No. 24. For final consideration No. 26 makes an excellent study of almost semi-natural grassland, close to Nos. 17 and 24, the soil conditions being similar except that No. 26 is in need of draining; No. 26 was originally Ling and Birch. The only factor which has altered it is grazing. Within recent times artificial manures have been applied but no lime. The bulk of the vegetation is Bent (57 per cent.) and Rushes (30 per cent.). Yorkshire Fog reaches 5.5 per cent., *Luzula* 2.5 per cent., and Meadow Grasses 2 per cent. The remainder is clothed with *Galium saxatile*, *Potentilla erecta*, *Prunella vulgaris*, *Hypericum humifusum*, *Anthoxanthum odoratum*, *Cynosurus cristatus*, with a few isolated plants of *Ranunculus repens* and *Trifolium repens* (Wild White Clover). Here once more we have an excellent example of how one deficiency may render grassland extremely poor. Remove that deficiency, and, other things being equal, the vegetation may be totally altered. Nos. 17, 24 and 26 make a most interesting trio, for the close relationship between the vegetation of the three is evident.

#### DISCUSSION.

It is evident from the temporary grasslands examined that the flora is determined first by the competition between the species originally sown and second by the advent of any interlopers which succeed in successfully gaining a footing in the artificial vegetation raised by the farmer. This competition is not a natural one since the sound management of grassland includes the maintenance of soil fertility, mechanical and other means of encouraging the

plants originally sown and discouraging interlopers, and a system of grazing which favours the formation of a good turf by the biting down of all plants present in the area. Climate, season, exposure and altitude may seriously interfere with one or more of these factors. Again, the modification or omission of any one of these factors which is within the control of the farmer immediately alters the *status quo* of the artificial association (9). If any one of the species sown occupies a greater proportion of the herbage than intended it will necessarily decrease the space occupied by one or more of the others. If the species which does this is short lived, and those which should have contributed the bulk of the herbage in later years have been crushed out, a weed or weeds may capture and even dominate the bare spaces left by the death of the shorter-lived species (18). Methods of overcoming this difficulty are not always practical or economic, and to this must be added the choice of grazing by stock. Stock exercise a distinct choice of food (palatability) with the result that weeds and less nutritious plants are neglected and nutritious plants may be overgrazed. The neglected innutritious species then spread because they are left to seed, or by vegetative means, the flora of the grassland changes to a more natural type, and the value of the grazing may become very low. Even on the best farms a prolonged drought or a very wet season may so upset the balance that it may be several years before the former state of the vegetation is recovered; sometimes it never returns to the same condition. In all such cases finance is the decisive factor, for obviously a farmer will not knowingly spend more money on a pasture than he can regain. Moreover, the stock question is all important, and if there is any difficulty in adequately stocking the grassland changes, often of a retrogressive nature, are bound to occur (10).

On the other hand, grasslands in a poor condition may be improved. Are such grasslands natural or are they old cultivated areas which have been allowed to revert? (26) Often the nature of the vegetation is of much assistance in determining this point. In natural or semi-natural grasslands (26) skilful and adequate grazing will often produce fine results. In some instances the only deficiency may be lack of phosphates (No. 21), although lime is also frequently deficient (Nos. 23, 24). Grassland which has arisen from old ploughland may be deficient in several plant foods. This state of affairs often leads, especially on higher ground, to a return to heath or scrub vegetation, and the same change may be met with even in the lower lying areas. Where the drainage of the soil is defective water-logged conditions soon arise, rushes spread rapidly (No. 26), and in time the grassland may develop into a marsh. Where grasses still remain the dominant species, the constant accumulation of vegetable matter may become faster than the rate of decay (19). Bent will certainly gain the ascendancy, with Yorkshire Fog, Sweet Vernal Grass, *Luzula campestris*, and many other species completing an almost natural association. As time goes on moss and lichens may follow till ultimately



*Sphagnum* may appear. Now it is the grazing factor that keeps untended grassland from changing to heath, scrub or woodland, for the really natural grasslands of Britain are probably very limited in extent (20). Mixed grazing produces the best result; grazing by one species of stock exclusively leads to well-known and clearly marked conditions of grassland. This can be illustrated by the state of the turf where rabbits are plentiful, for the rabbit-grazed areas have a distinctive appearance and turf (7). It is also evident from No. 25 that allowing the grass to grow tall and cutting for hay is quite different in its results from the short cropping of grazing. Consequently the factor of first importance is a biotic one—the grazing of animals.

The flora of some permanent, semi-natural and natural grasslands presents many problems. Their past history is important but frequently unknown. Occasionally these grasslands are broken up and resown successfully (13 b), sometimes a renovating mixture is used (14), and in not a few cases increased grazing can produce wonderful results (8). The difficulties are lack of soil aeration, deficiency of one or more plant foods and most frequently inadequate grazing. A herbage which is well grazed and not allowed to grow to length is far more nutritious, as has been recently shown (28). The importance of grazing and its rôle in the improvement and future treatment of grasslands has not always been sufficiently realised. It does much to decrease the long list of plants present in some of the semi-natural grasslands. Many of these plants have a value in poor grassland, but are considered weeds in good grassland. Bent, Yorkshire Fog, and a few other inferior grasses and dicotyledonous plants have some value in such cases. Which plants are to be considered as weeds is a difficult problem, as has been indicated by Brenchley (2). The reduction or suppression of many of these inferior plants is difficult, owing to their ability to propagate themselves by vegetative means (17), Bent being a very good example (3). It is often one of the biggest problems in improvement. The condition of the soil frequently assists the less nutritious plants. Acidity is one of the most common causes of inferior vegetation. Sorrel and other calcifuges flourish and spread, not because they prefer acidity but owing to the more nutritious grasses and clovers being unable to offer any competition (22). This is well illustrated by Nos. 23 and 24.

There are a few individual species whose presence calls for some comment. The disappearance of Field Mint (*Mentha arvensis*) after the application of lime and road compost (No. 23) may suggest competition as the chief cause. Competition comes in, but a more fundamental cause is at work. Mint may remain in grassland in spite of grazing and cutting. Liming, however, alters the physical and chemical conditions in the soil, altering those factors helpful to Mint and favouring grasses and clovers. It is often associated with poor drainage or an impervious layer some distance below the surface soil, a state of affairs readily altered by liming.

Gorse (*Ulex europaeus*) is another example of a plant which is much



affected by liming, as is shown by the case of No. 24. There were plenty of seedlings and young plants in the unlimed part of the field. Here again the cause is not entirely a question of competition. It is the change in soil conditions which react adversely on the seedlings and young plants of Gorse, lessening their chances of survival and successful competition. In most instances where Gorse is found growing the soil has an acid reaction. It is not a plant which is readily eaten, so that grazing is not the solution of the problem. The increased growth of grasses and clovers, however, does affect it very much, since their more luxuriant growth tends to shade out the Gorse seedlings.

Greater Bird's Foot Trefoil (*Lotus major*) is another very interesting case. It will be noted that in Nos. 22 A, 23 A, 24 A, and 26 this plant is present in the unlimed soil, but disappears shortly after liming. The success of this *Lotus* in long, coarse, and tufted vegetation is due to its ability to send up long, slender stems to the light, when other legumes are shaded out. One might therefore expect that it would (being a legume) show to still better advantage when soil conditions are improved. It seems, however, that it is not very sensitive to acidity and adverse conditions. In 1927 it was sown across strips of very acid soil treated with lime, kainit, sulphate of ammonia, basic slag, and "complete minerals" respectively as well as on untreated soil. The area was originally a Nardetum type of vegetation on the southern basal slope of Caerketton, the elevation being about 1100 ft. At the end of the year and throughout the growing period *L. major* showed no appreciable difference in growth across the treated strips. Red and White Clovers showed marked differences and even *L. corniculatus* varied in growth according to treatment. Alsike Clover showed much less response to different treatments than the other clovers, which is in keeping with its presence in 23 A. Hence it seems that *L. major*—at least under certain conditions—does not show a marked response to manurial treatment. In this connection it was noted that in the grasslands of Devonshire where grazing was not close or intense *L. major* was frequently the only legume present in some of the poor grasslands. Again, where manurial treatment was tried—chiefly with phosphates—the first stage in improvement was marked by a luxuriant growth of this plant. Later it completely disappeared and Wild White Clover with some of the more nutritious grasses dominated the vegetation. In other words, it represented a certain phase in the floral succession of grasslands. It seems, therefore, that lime has not a very marked effect on *L. major*, but lime with other manures may stimulate other plants which are then more readily grazed. The grazing adversely affects *L. major*, whose recovery after eating down is relatively slow. Thus it is the combined effect of competition and grazing which crushes it out, and not the direct effect of liming.

The presence of *Viola tricolor* in grasslands is not unusual, for in many of the poorer grasslands it is plentiful where the soil is light and rather acid. Another situation where this plant tends to appear in quantity is on dry sandy

banks after Whins (*Ulex europaeus*) have been burned down. One of the first plants to colonise the ground after the fire may be *Viola tricolor*. In parts of Aberdeenshire and Kincardineshire, we have seen *Viola tricolor* form an almost closed community following the destruction of Whin areas by burning. It is soon overwhelmed by other plants, but its short dominance was a well-marked phase in the colonisation of the bare space after burning. Its presence in grassland also represents a phase in the development of the vegetation. As soon as soil and other conditions are altered it rapidly diminishes in numbers or may completely disappear, as shown in the case of No. 23.

It is evident, then, that although the geological formation and the nature of the surface soil may be a decisive factor in determining the flora under natural conditions, this is not necessarily true of all agricultural land. The marked similarity of some of the grasslands, both temporary and permanent, in different parts of Scotland, where the elevation and geological formation are different, is very noticeable. This is due not only to the biotic factor but to the making good of any deficiencies in plant foods which primarily existed in these soils before agriculture altered them. It is another of the many instances where natural factors may be completely altered and the result reflected in the vegetation.

The botany of grasslands presents a whole series of such ecological problems. These problems are complicated by the fact that so many artificial factors are introduced, modifying and often completely changing the natural condition and tendencies of the vegetation. There are many interdependent factors most difficult to assess at their true value. Hence it is that such problems are becoming more and more of a separate study in themselves. From the few examples studied it is evident that there is much work still to be accomplished, and that many of our poor grasslands will make a good response to sound treatment. That it can be done is evident from several of the examples quoted. There is only one thing that may render improvement impossible, and that is the question of cost. When cost is the deciding factor, as it often is at present, then the Botanist after doing his part must hand the problem over to the Economist.

#### SUMMARY.

Provided soil conditions are good, the success of grassland of short duration is chiefly dependent on the sowing of a well-balanced seed mixture. In consequence these grasslands generally show a strong similarity in flora.

The use of an inferior strain of any species, such as White Clover (*Trifolium repens*), may cause marked changes in the flora and the proportion of the species present.

As grasslands grow older—unless badly treated—the floral changes are gradual and tend to follow the persistence of the species sown. *Trifolium repens* (Wild White Clover) covers more ground, as also *Dactylis glomerata*,

*Poa trivialis*, and perhaps *Phleum pratense*, while *Lolium perenne* tends to decrease to a more stable proportion.

Cutting more than one hay crop may have disastrous results in depressing and even killing the more important turf-growing species. The resulting grassland may in consequence become bare and full of weeds.

In grasslands of long duration, soil conditions and general treatment play a very important part; grazing is a most important biotic factor. Deficiency of nitrogen, calcium, phosphorus or potassium, or of more than one of these, is reflected in the flora of the grassland.

Where the grazing and general treatment of old grassland has been continuously sound, the vegetation is often restricted to a small number of species, and the flora shows a strong resemblance to that of short-duration grasslands on soils of high fertility.

The accumulation of undecomposed plant remains and poor drainage are immediately reflected by the typical flora of grassland so affected.

The marked and swift changes in the flora of many grasslands when any marked soil deficiency is removed and grazing is adequate provide an interesting ecological study of great practical importance.

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# PRELIMINARY WORK OF A NEW BIOLOGICAL STATION (LOUGH INE, CO. CORK, I.F.S.)

By LOUIS P. W. RENOUF.

(With Plates XXIII-XXVI and 3 Maps.)

## HISTORICAL.

MR RICHARD SOUTHERN, of the Fisheries Branch of the Department for Agriculture and Technical Instruction for Ireland, whilst on a cruise for the Department, spent five days collecting specimens and making observations in Barloge Creek and Lough Ine or Hyne, into which it opens, during November, 1916.

So interesting did this area appear to be, from the data collected during this short time, that the Royal Irish Academy formed the intention of investigating it in detail, as soon as times were normal again. Post-war conditions, however, altered the outlook of even this long and firmly established body, and the matter had to be shelved.

This was briefly the introduction to the district which Dr R. Lloyd Praeger gave the author during 1922 on the first occasion they met, some little time after the latter had taken up duties at University College, Cork; and with it was coupled a strong suggestion to the effect that, as it was within easy access of Cork, the author should begin its investigation.

A visit to the district was made during the following February, 1923, and though for the three days of its duration rain was incessant, the inducements met in other directions were such as to make the author resolve to follow Dr Praeger's suggestion, and arrangements were made to spend part of the following Easter Vacation at Baltimore, where the nearest accommodation was available.

During this first fortnight a very general idea of the Baltimore-Lough Ine region was obtained, and more or less permanent quarters were found at Baltimore. These were used as headquarters during the Summer Vacation and a "Survey" was started. This very soon showed that Lough Ine would be an ideal situation for a laboratory to be used as headquarters, from which to carry out the contemplated survey of the Carbery Region. In the complete absence of funds and in view of the apparent impossibility of obtaining accommodation of any kind at Lough Ine, prospects, however, were not very bright.

But the very next year a small bequest left by Miss E. Crawford Hayes, for the promotion of biology, became available, and the Governing Body of University College, Cork, agreed with the suggestion that some of this should be spent on the proposed work. During March, 1925, a large room was rented and used as a laboratory at Baltimore, and a really serious start was made.



Gradually the shyness of the farmer holding Barloge, the key to Lough Ine, was overcome, and short stays were made at the farm. These culminated in the obtaining of permanent living accommodation at Barloge, and the installation of a very large packing case in a sheltered situation alongside the Narrows, between Barloge Creek and Lough Ine itself, for use as a laboratory, during 1926. This was the condition of things for some three years, during which Baltimore was used as headquarters, Lough Ine as a field station.

1928 saw the erection of an army-hut type of building which was fitted out as a laboratory and aquarium alongside the Narrows, and an intensive study of Lough Ine and its immediate surroundings was started. Reports of what we were doing and of the richness of the area from the biological aspect prompted enquiries from other universities, as a result of which a second larger laboratory, with simple feeding and lavatory accommodation was erected and equipped (Plate XXV, Phot. 11). This has been used by visiting classes and individual workers each Easter and Summer Vacation since, classes preferring the former. In consequence our ambitions have increased, and we hope eventually to see the Cork University Biological Station firmly established as a fully recognized station, and to extend our operations over a much wider area than that originally contemplated. A second consequence of this unexpected development is that the amount of research work accomplished so far, by the station itself, is not so great as it would have been had the necessary time not been given to organising the arrangements for visiting workers, and on this hangs the need for publishing this general account of what has been done, that it may serve as a guide to what we hope will be done in the near future.

DISTRICT INVOLVED (SEE MAP I, p. 412).

The wider area referred to above is roughly 20 miles wide by 32 miles long, and lies between Bantry and Dunmanway to the north, Bantry and Mizen Head to the west, Mizen Head, the Fastnet Rock and Glandore to the south, Glandore and Dunmanway to the east; in other words it embraces the greater part of the old barony of Carbery.

Of the 600 and odd square miles enclosed by these lines the sea and tidal estuaries account for some 250, land and fresh water for some 380.

The land area includes a great deal of hilly country, especially to the west and north, with ranges of hills stretching roughly from Glandore to Dunmanway—highest point 986 feet; Dunmanway to Bantry, with Owen (Nowen)<sup>1</sup> Hill 1763 and 1673 feet, Derreenacrinnig 1330 feet, Mullaghmesha 1629 feet; Bantry to Sheep's Head, with Seefin 1139 feet, to Mizen Head, with Milane Hill 1160 feet, Mount Gabriel 1339 feet, and Knocknamaddree 1034 feet. Most of the river valleys between these are small and represented mainly by narrow strips and small areas between the ranges and the sea. The valleys of the

<sup>1</sup> Cnoc Owen—the Hill of Streams. The Ilen, the Bandon River and the Meallagh (Bantry) River all arise here.





River Ilan and its tributaries, with Skibbereen as their centre, form exceptions to this rule however, and radiate out to Union Hall, Leap, Drimoleague, Baltimore, and Ballydehob, Schull, and Crookhaven, the islands north of Broad Head and Cape Clear being the remnants of a delta, which lay in the mouth of an originally bigger river, of which the Rathruane and the Banacknockane at Ballydehob, and the Leamawadda and others were tributaries.

#### GEOLOGY.

The greater part of the Carbery region consists of Old Red Sandstone, through which run bands of Carboniferous Slate, the general direction of the formations being south-west, and the bands alternating with each other in their general arrangement.

The Baltimore-Lough Ine district is nearly all Lower Old Red Sandstone; a belt of Carboniferous Slate, about 2 miles wide, lies to the north, and passes from Roaring Water Bay, through Skibbereen and Leap. Other belts border Dunmanus and Bantry Bays, the former becoming wider as it is traced inland, its southern limit lying about a mile to the south of Drimoleague and converging towards the more southern belt mentioned above.

#### PRESENT SPHERE OF OPERATIONS.

Up to the present work has been confined to the more or less immediate neighbourhood of Baltimore and Lough Ine, special attention having been paid to Lough Ine itself. Although a great deal of work has been done, none of it can claim to be in any way complete, except in so far as it has amply confirmed the original expectations that the area would prove to be of exceptional interest.

This interest is presented not only by the variety of habitats within a very small radius and the richness of the fauna and flora they support, but also especially by the varied problems which many individual species and associations offer. In addition to the more purely academic problems suggested by many of the habitats and associations, both plant and animal, a problem of first class importance is afforded by the changes which have taken place in the larger marine fauna. These have resulted in the failure of a considerable hake fishery, which was carried on from many centres along the coast; a lucrative pilchard industry, whose headquarters were at Baltimore and Bantry; and oyster fishing, from beds in Lough Ine, between the islands in Baltimore Harbour, and elsewhere. Hake and pilchards seem to have deserted the coast; oysters have been suffocated by silt or have perished through other agencies. So far as Lough Ine is concerned *Asterias glacialis* L. and *Nassa incrassata* (Stroem.) may have been the culprits, though probably the low temperature of the water has been another factor.

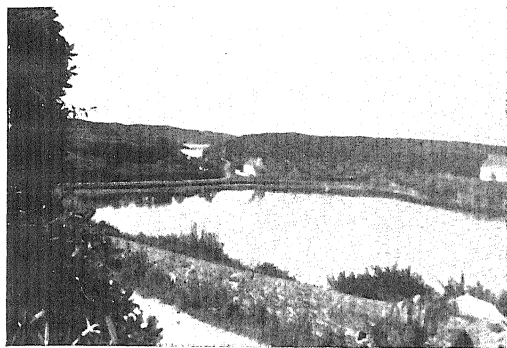
## GENERAL FEATURES OF THE REGION (SEE MAP II).

The whole district around Baltimore and Lough Ine consists of unevenly undulating country, much of which is rugged in the extreme (Plates XXIII-XXVI, *Phot.* 3, 4, 7-10, 11, 14). Pockets of very fertile soil occur, but most of the fields are small, the majority under two acres, and even in these large outcrops of rock are frequent. The ground rises rapidly from the sea, the rise along most of the coast east of Baltimore Harbour being very steep, often practically sheer, while the coast throughout the region is very rocky. Beaches are numerous, owing to the indented nature of the coast, but for the most part they are composed of boulders and pebbles, and are very small in extent. Sandy beaches are of rare occurrence, the chief ones being Tranaplousa and Tragowenmore on the west of Sherkin, and Tragumna or Tragemona (see Plate XXV, *Phot.* 13) to the north of Gokane Point and east of Lough Ine. Caves, the majority of them small, occur in many places, and subterranean passages, through which the sea ebbs and flows, pierce Kedge Island and the headland of which it once must have formed part.

By far the greater part of the area consists of moorland (see Plates XXIII, XXIV, *Phot.* 3, 4, 7), interspersed with marshes, marsh ponds (Plate XXIII, *Phot.* 5, 6), peat bogs, bog ponds where the peat has been cut, and small lakes. Many interesting transitions from one to the other occur. Of the lakes Lough Ballyally, some 9 acres in extent, is the largest, Lough Nacartan, about 2 acres, is probably a large bog pond, while the lough at Tragemona, 2 acres, promises to prove of special interest because it is liable to wave effects at spring tides during south-west gales.

The River Ilen is tidal to just above Skibbereen, but the main channel is narrow and its navigation difficult. Boats up to 50 tons still, however, ply as far as Skibbereen, which is a very important distributing centre. In the estuary proper the river is divided into two very unequal arms by the islands of Inishbeg, about 100 acres, and Ringaroga, about 900 acres, the eastern one of which is reduced at low water to a small stream meandering through a mud flat and between countless rocky islets. The southern shore of Ringaroga and the smaller Spanish Island, separated from its south-western extremity by a very narrow channel, form the northern boundary of Baltimore Harbour, whose western limit is determined by the eastern shore of Sherkin Island. The channels leading into the harbour from the Atlantic on the south, between the mainland and the south-east of Sherkin, and between the north-east of Sherkin and Spanish Isle, are very narrow, whilst the former contains a sunken rock—the Loo—marked by a buoy. The channel is marked at night by a lighthouse on Sherkin and a white beacon on the mainland on to which it flashes.

Sherkin Island is very irregular in shape by reason of the large bay known as Kinish Harbour, which nearly divides it into three. South-west of it lies Cape Clear Island, the southern point of which is usually described as being the



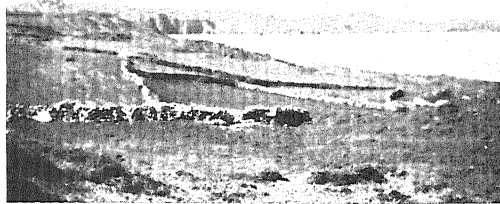
Phot. 1. Baltimore. Cove Bay at high water. Tranadroum and Sherkin in the background. Sheehan's Island is the rising ground behind the two cottages.



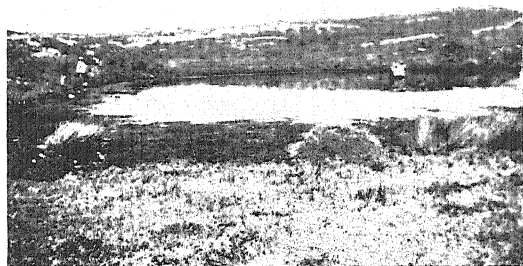
Phot. 2. Baltimore. Cove Bay at low water.



Phot. 3. Baltimore. Typical country.



Phot. 4. Baltimore. On the way to the Beacon. Sherkin in the background.



Phot. 5. Baltimore. A marsh pond, normal condition.



Phot. 6. Baltimore. Same pond as phot. 5, after an exceptionally dry spell.

RENOUF—PRELIMINARY WORK OF A NEW BIOLOGICAL STATION (LOUGH INE, CO. CORK, I.F.S.)





most southerly point of Ireland. Actually, however, this honour belongs to the Fastnet Rock<sup>1</sup>, which lies some 3 miles south-west of the usurper. Between Sherkin and Cape Clear and the peninsula running south-west and ending in the Mizen Head are numerous other islands and islets. The largest of these are Hare or Heir (about 380 acres), the three Calf Islands (together about 200 acres), and to the north-west of these Long Island (300 acres), Castle Island (120 acres) and Horse Island (155 acres), which are said to have formed one long island until the middle of the ninth century. North-west of these is Roaring Water Bay, whose name is elegantly descriptive of the conditions which prevail there during a south-westerly gale.

#### BALTIMORE DISTRICT.

*Coast.* The coast from the inner harbour round to the Kedge Rocks is very much indented with small bays and gulfs. Two of these are especially worthy of mention, because they contrast very strikingly with each other. They are the Cove and Tranadroum (Plate XXIII, Photos. 1, 2), both within Baltimore Harbour and separated from each other only by a low-lying strip of land some 26 yards wide by 235 yards long. According to local tradition the high ground, composed mostly of rock, which forms their north-western boundaries and which is known as Sheehan's Island, was actually an island until the Spaniards who established a pilchard industry here joined it to the mainland. (The holes into which poles were put during the process of extracting oil from the fish are still quite plain—see Plate XXIV, Phot. 9.) The floor of the Cove is of mud, intermingled with sand and covered with boulders and stones along the south-east and south-west, whilst a small stream enters at the southern corner. Its fauna, therefore, includes burrowing Molluscs and Polychaetes, such as *Mya arenaria* L., *Tapes virgineus* L., *Cardium edule* L., and *Arenicola marina* L., which are dug for bait, the daisy anemone, *Cereus pedunculatus* (Pennant), and the sea-squirt, *Phallusia mentula* (O.F.M.), growing in large numbers on small flat stones embedded in the mud, and tube-making Polychaetes, such as *Sabella pavonina* Sav., *Branchiommia vesiculosum* (Mont.), and *Myxicola infundibulum* (Ren.), which burrow between these stones.

The main part of Tramadroum is of rock and pockets of coarse sand, but its upper region is covered with stones. Ridges along its south-western and boulders along its north-western sides provide shelter for a very different fauna from that found even on the rocky parts of the Cove. The most interesting members are the Gephyreans *Phycosoma granulatum* (Leuckart) and *Thalassema neptuni* Gaertner, and the Hemipteran bug *Aëpophilus bonnairei* Sig., all of which live in crevices in the schist. *Aëpus robinii* Laboulb., a beetle, which lives in crevices in boulders which are exposed only at low water of spring tides, although it is, like *Aëpophilus*, an air-breathing form, is found in the Cove as well.

<sup>1</sup> The Irish name for the Fastnet, Carrigeena (more correctly Carrigaonair), means "the lone rock."



The flora of Tranadroum is much richer than that of the Cove by reason both of its conformation and of the fact that it is more exposed to wave action. A complete study of these two bays is in progress.

From Baltimore seawards the ground rises and the whole of the coast is very rugged, in many places sheer. These characters are well seen at Beacon Point, at the entrance to the harbour, where there are sharp ridges, deep gullies and caves, which support an abundance of life. At low water of spring tides the edible sea-urchin, *Echinus esculentus* L. is exposed in large numbers, together with forests of *Laminarias* and carpets of *Florideae*. Cliff plants include *Crithmum maritimum* L. and varieties of *Anthyllis*.

*Inland.* The greater part of the land consists of undulating gorse-heather moor with outcrops of rock in abundance, small fertile patches, most of which are used to good advantage, and marshy patches, often with pools (Plate XXIII, Photos. 5, 6). These marshy regions are of very great interest because they not only bear different dominant plants, *Hypericum elodes* L. here, *Iris pseudacorus* L. there, *Osmunda-Juncus* elsewhere, and so on, but also show transitions from one type of association to another, different stages in reclamation and in reversion. The ponds contain large numbers of aquatic animals, *Nepa cinerea* L. the water scorpion, and *Argyroneta aquatica* Latr. the water spider being especially noticeable. Frogs are scarce, but the common newt, *Molge vulgaris* L. is abundant. On several occasions this last has been found in "dug-outs" beneath boulders on the shore which were within the reach of spring tides.

The more noticeable plants include *Pinguicula vulgaris* L., *Spiranthes spiralis* Koch and *Rosa spinosissima* L.

*The Islands. Sherkin.* Sherkin is not only the largest of the islands, some 1250 acres in area, but also probably the most interesting on account of Kinnish Harbour, which all but cuts it into two and which at low water exposes large mud-flats, its caves, and particularly the sand at Tragowenmore and Tranaplousa on its southern coast. *Glaux maritima* L. sea milkwort, and *Suaeda maritima* Dum. sea blite, grow well here above high-water mark, whilst *Eryngium maritimum* L. sea holly and *Viola curtisii* Forst. occur among the grass on the blown sand above the bays. *Helix pisana* L. the sandhill snail occurs here in large numbers. The common shore molluscs, especially *Littorina rudis* (Maton), *L. littorea* (L.) and *Purpura lapillus* (L.), exhibit great ranges in shell variation, as regards both colour and texture, on the rocks of Tranaplousa, where they occur in great numbers. Another striking feature of the fauna is the occurrence, at times, of the lamp Polypes, *Lucernaria campanulata* Lamour. and *Halicystus auricula* Fabr. on *Chondrus* and *Ulva*, their normal habitat being *Zostera*. The outstanding record from the other islands is that of a single specimen of Ray's bream, *Brama raii* (Cuv.), which came ashore on Hare Island during the summer of 1927, and which was passed on by its captor Stewart Musgrave, Esq., of Cork.

*Roadsides.* Roadsides present a great diversity of habitat. Hedges of

*Fuchsia*, *Crataegus*, *Fagus* or *Ligustrum*, dykes of stone or turf, ditches, streams, and marshes and bogs with ponds. An interesting contrast is afforded by the roads along the eastern and western sides of Lough Ine. The former is entirely devoid of trees, the latter bears trees on both sides, some of them meeting each other high overhead, while water trickles down the walls of rock, which form its western boundary in many places, to form a small stream. The vegetation here includes at least sixteen species of fern, including *Osmunda regalis* L., liverworts, lichens and mosses in profusion. Of the lichens *Peltigera canina* Ach. in association with other species of the same genus, is one of the most obvious. On account of the mildness of this situation several forms make very early appearances during most years. As examples may be cited a particular *Quercus sessilis* Ehrh., which is usually in leaf by about March 20th, and the occurrence of frog spawn during the first days of February.

The eastern road is beginning to show a transition in its vegetation, on account of flooding at high spring tides, through breaks in the sea wall. This latter is carpeted with lichens and mosses, but one of the chief interests of this side centres around two small ponds, which are separated from each other by only a few yards of rock. One of them, fed only by rain and land-drainage, supports a meadow of *Glyceria fluitans*, in which frog spawn develops. The other derives its water supply mainly from the Lough, whose water seeps through under the road at high tide. Its vegetation consists of *Enteromorpha*, *Fucus spiralis* and small green algae. The sides of the pond support a typically littoral flora, including *Statice*, *Salicornia*, *Suaeda*, *Cochlearia*, *Plantago coronopus* and *maritima*, and *Triglochin maritimum*. Along its northern and eastern sides grow various species of *Juncus* and *Carex*.

LOUGH INE OR HYNE (see Map III). (Plates XXIV-XXVI,  
Photos. 7, 8, 10, 11, 14.)

Lough Ine or Hyne lies on the old Skibbereen-Baltimore Road, about half-way between these two places, and some 4 miles from them. There are two traditions about the name of this piece of water. Of these the one associates it with the little holy well of St Ina, a few hundred yards up the Scour Road, on the way to Creagh. The other refers to the popular belief that the Lough is bottomless, and derives the name from "doimhin" (pronounced rather like "ghine"), which means "deep."

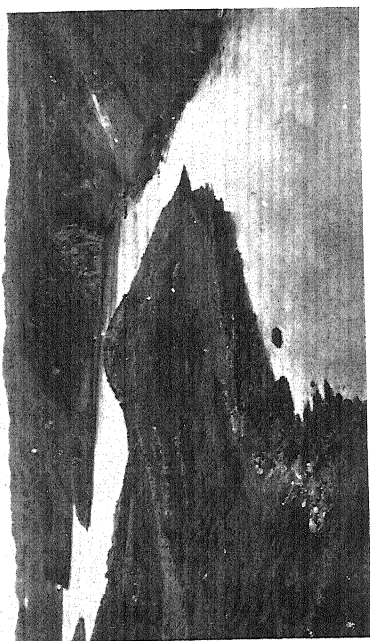
Though the Lough proper is but three-fifths of a mile long by three-eighths of a mile wide, its different parts present widely differing physical, and therefore correspondingly different biological, features. Roughly rectangular in shape Lough Ine is land-locked, except at its south-east corner, where a narrow channel some 26 yards across its widest part, puts it into communication with the Atlantic Ocean, two-thirds of a mile farther south, via a wider channel, Barloge Creek, which broadens considerably opposite Tranabo Cove, with which it is joined at high water (Plate XXIV, Phot. 10).

The physical feature which most affects the Lough is a rocky sill (Plate XXIV, Phot. 8), about 6 feet high, situated at the narrowest part of the channel—usually referred to as the Narrows or the Rapids—on account of which the ebb and flow in the Lough do not synchronise with these changes in the sea without. Through the narrowness of the channel there is a lag at the beginning of the ebb tide, but far more important than this is the fact that on account of the Sill, the Lough continues to ebb for a long period,  $3\frac{1}{2}$  hours during neap tides, after the beginning of the flood tide outside. During spring tides this period is much reduced owing to the fact that these tides reach the level of the top of the Sill, and there meet the ebb tide from the Lough much sooner than do the neap tide floods. Hence it follows that the lowest ebbs from the Lough occur at the times when the outside ebbs are at their minimum, and that there is very little ebb from the Lough when they are at their maximum. A second very important effect of the Sill and the Narrows combined is that the flood water entering the Lough and the ebb water descending into Barloge Creek is first of all confined and then suddenly released, with the result that it is very turbulent and consequently very highly aerated.

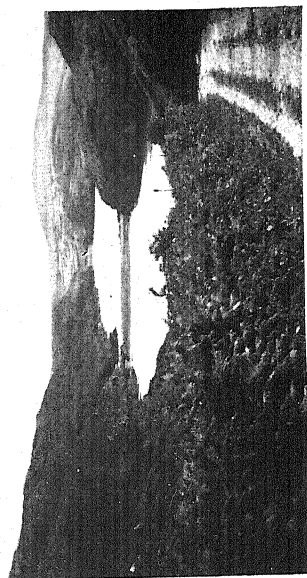
The surrounding land is all high and steep, the peninsula which forms the southern boundary of the Lough and the western boundary of the Rapids and Barloge Creek being less so than the rest. In spite of this no considerable body of fresh water enters the Lough, the largest being the two streams already mentioned as entering at the north-eastern corner, and near the north-west quay, and another small one which flows into the western corner of the Goleen<sup>1</sup>. Apart from these there are only slight trickles down the face of the rocks in various places. At times of heavy rain, however, the amount of fresh water which drains into the Lough must be very considerable. In fact Southern reports that he found a considerable layer of fresh water, without any taste of salt, overlying the salt water, a phenomenon which we have experienced in a lesser intensity.

*Habitats.* The number of strikingly different habitats afforded is very surprising, especially when we reflect that the whole Lough covers only about a quarter of a square mile. This variety is due to four chief factors: the rocks, which form the boundary of the greater part of the Lough are broken into in many places, with the formation of small bays, and stone and boulder beaches; an island, Castle Island, shaped something like a figure of eight, lies off the southern and eastern shores; the south-western corner opens into a pocket, extending southwards for some 400 yards as the Goleen, which besides being very shallow contains a few small islets; and the bottom, in addition to shelving very differently along different parts of the shore, undulates considerably, and exhibits considerable differences in its composition. Over a wide belt, which extends from the north-west quay to the north quay, the bottom is of hard sand and slaty stones, with a good many boulders in

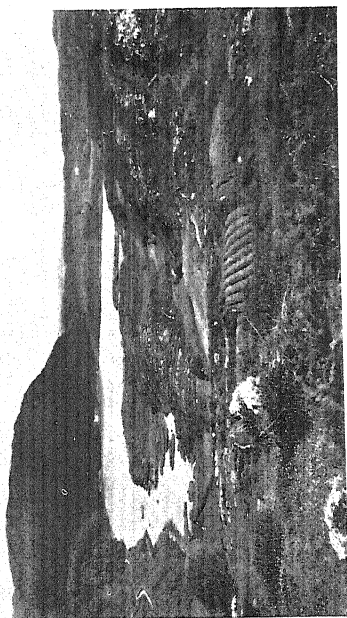
<sup>1</sup> From "goilin," a pool or a little back harbour.



Phot. 8. Lough Ine. The Rapids and Southern's Bay.



Phot. 10. Lough Ine. The Coosh at low water. Tranabo Bay behind, Bullock Island to the right.



Phot. 7. Lough Ine and Barloge from the South.



Phot. 9. Sheehan's Island between Cove Bay and Trana-droum. Rocks showing holes for Pitchard Presses.

RENOUF—PRELIMINARY WORK OF A NEW BIOLOGICAL STATION (LOUGH INE, CO. CORK, I.F.S.)





places, and slopes more or less gradually. Off some of the bays and beaches too the slope is a gradual one. Off most of the rocky regions, on the other hand, the slope is very steep and in some cases the drop is sheer. This last is true also of some of the beaches, whose fringes are formed by slabs and boulders, particularly where these have been cemented together by calcareous organisms. Where the depth exceeds 10 fathoms the bottom is usually made up of very fine mud. In places where the shelving to this depth is gradual the bottom is harder, generally of a coarse sand, and is covered with rough stones and shells. This is true especially of parts along the eastern and western shores. In many places the sand is covered with a carpet of a very fine species of *Callithamnion*, which makes washing out the sand very difficult, as it continually blocks the sieves.

Grab samples have been taken in various places to supplement the general information obtained by means of the dredge and the trawl, but the bottom is so irregular that a great deal more work of this kind and several thousand soundings will have to be taken before it will be possible to make even a rough map of it.

Soundings (some 1200 have been taken) show that although the north-eastern part of the Lough is covered by 10 fathoms and less of water, and the Goleen proper by half a fathom on the average, most of the rest has a much greater depth, the average being about 20 fathoms. The deep region lies roughly between lines drawn from marks 11 to 42 and from 16 to 40 through 5 Castle Island. The maximum depth,  $32\frac{1}{2}$  fathoms (59.2 metres), occurs just north of the entrance to the Goleen, and lends some slight support to the legend which derives the name of the Lough from doimhin, for this is a surprising depth to occur in such an area.

*Other Physical and Chemical conditions.* As already pointed out, one of the most interesting points about the Lough is the fact that owing to the height of the Sill in the Rapids above the bottom seawards of the Narrows, the lowest ebbs from the Lough occur at the times of the smallest neap tides. In order to determine the maximum ranges of the tides, both in and below the Lough, graduated posts have been planted at the northern corner, in the Goleen, in a little bay (referred to as Scyllium Bay, shore region S.13 on Map III) on the south shore near the Rapids, and at the south-western point of Southern's Bay. Readings taken from these show that, while the maximum difference between low and high water in Southern's Bay is some 12 feet, in the Lough it is rather less than 4 feet. (During winter gales, when the Lough is very tempestuous, wave action reaches considerably further than these figures suggest.) The positions of the tide posts are indicated on the map thus A B C D.

Though only a little hydrographical work has yet been possible the results obtained are sufficient to show that only the surface water to a depth of something under 10 fathoms is directly affected by the tides, but that the whole of the water in the Lough, which is more or less regularly stratified, is subject to



seasonal changes. This is shown by the following figures, which give the average temperature, specific gravity (surface), and pH for September, 1928, and April, 1929:

	Temperature (° C.)	Specific gravity	pH at room temperature
September, 1928			
Surface	15.5	1027.5	8.4-8.5
20 metres	14.8		8.3-8.4
30	12.0		8.0-8.1
40	10.2		8.0-8.1
April, 1929			
Surface	11.0	1025.5	8.4
20	9.6		8.3
30	9.5		8.3
40	8.0		8.0-8.1

The figures for specific gravity show the effect of the winter rains. A sample taken during February, 1930, at the time of a south-west gale gave a reading of 1024. To the taste it was saltless, but no doubt this was because of the amount of fine spray which was being blown about and which must have affected one's lips and critical sense of taste.

The amount of work done on salinity and alkalinity is insufficient to lead to any conclusions, but the results obtained do suggest that in some parts of the Lough the fresh-water streams retain their individuality for some considerable distance from the shore. This may be of importance in connection with the distribution of Diatoms.

For the purpose of having standard cross-bearings during sounding, water-sampling, dredging, etc., the rocks have been blazed in suitable places with patches of white paint. These are indicated on the map by means of circles, each of which contains a fixed number.

*Biology.* From the biological standpoint the outstanding features are the relative absence of the larger algae, the abundance, especially in certain localities, of encrusting Corallinaceae, and the extraordinary plentifulness of animals, in particular of sedentary and sessile forms, coupled with the occurrence in very shallow water of more or less typically deep-water species.

*Botany.* Though the zoning of the lichens and algae is masked in a great many places, on account of the irregularities of the shore, and of the narrowness of some of the zones, it can be made out quite well on the whole. *Fucus serratus* L., however, occurs in only a few places.

Where fresh water enters *Fucus ceranoides* L. occurs, in amounts roughly proportional to that of the fresh water, if largish stones are present to afford it a suitable substratum. In their absence the presence of fresh water is indicated, as is usual, by the growth on *Enteromorpha*.

Laminarias are absent from most parts of the shores, but occur to some extent on the rocks at both ends of the island; between the eastern end of the island and the mainland, on rocks which are exposed at low water; on the rocks north of the Rapids, and in the mouth of the Rapids *Laminaria saccharina* L.

is the common species, with *Laminaria digitata* L. and *Saccorhiza bulbosa* De la Pyl. in addition in the Rapids, where *L. cloustoni* Edm. also occurs.

*Enteromorpha* and *Ulva* occur more or less abundantly and spasmodically, the former where fresh water influence is at work, the latter mainly below the *Fucus* zone, whilst *Himantalia lorea* Lyngb. is common in what should be the Laminarian zone, in those places where Corallines are not excessive in amount.

Corallinaceae are exceedingly abundant, as compared with the other kinds of algae present, and are largely responsible for the character of several regions of the shore. Along several stretches on the west, the east and the south, they (together with Porifera and other sessile animal forms) cement together the boulders and rock fragments, the effect produced in some places being that of a fringing shelf of conglomerate, varying in width from 2 to 10 feet or more. This effect is best seen about the middle of the southern and in two regions of the western shores. The greatest quantity, however, occurs along the middle region of the northern shore of Castle Island, where a *Melobesia* dominates a zone of from 10 to 30 yards or more, encrusting stones and shells with a thick tuberculous coating, whilst a thin and somewhat leaf-like form (*Lithophyllum lichenoides* Ellis) constitutes a conspicuous feature of Scyllium Bay, where it is exceedingly and painfully abundant, both on the boulders and on other algae growing on them. Its presence interferes very considerably with shore collecting, owing to its razor-like cutting powers.

A further feature of the algal distribution is the presence of what may be described as small fields of *Cystoseira ericoides* C.Ag., at the south-eastern corner and on the north-east of the island, and in smaller patches on the eastern shore, just in front of the Narrows. It will be observed that all these situations get the full benefit of the in-rushing tide.

A remarkable contrast with the abundance of Corallinaceae and paucity of Laminariaceae in the Lough is provided in the upper part of Barloge Creek, referred to as Southern's Bay, where the latter are abundant, the former very poorly represented. A further contrast is presented by large meadows of sea-grass, *Zostera marina* L., which carpet the whole floor of the upper half of the Creek, with the exception of the main channels, which are very narrow. *Zostera marina* does occur in small quantities in some parts of the Lough, but these cannot be described as meadows; on the other hand, meadows occupy the greater part of the floor of the southern half of the Goleen. These, however, are composed of *Z. nana* Roth.

*Zoology.* The most conspicuous animal form is *Paracentrotus lividus* (Lam.), the spiny purple urchin, which occurs abundantly in most places where the substratum is really hard, with the exception of those which are subject to the full force of the incoming rush through the Narrows, and where the rocks are sheer. So plentiful is it in some places that twenty adults may be found in a square foot, which contains numerous small specimens too. In some places, especially along the southern shore, the olive green variety occurs mingled with

the deep purple form. It is noticeable also that specimens from different regions exhibit very great differences in the length and robustness of their spines. In two places, one on the eastern shore, the other on the northern shore of the island, *Paracentrotus* lives in excavations in the rock, as described by Nicholls in the Clare Island Report (57, p. 8). It also moves up and down the shore with the flood and ebb tides, and is very prone to cover itself partially with empty bivalve valves, those of *Anomia* being its especial favourites, but possibly only because they are particularly abundant.

Were the individual *Anomia ephippium* L. equally conspicuous with the individual *Paracentrotus* this species would be the outstanding inhabitant of the Lough, for not only is it exceedingly plentiful in the living state, literally encrusting stones and boulders in many places, but its valves cover large areas of the bottom.

*Pecten varius* L. is the other outstanding Mollusc, and is especially abundant on boulders along the north-west, most of the north shore, in various places along the west and south, along half the north shore of the island, and in the northern part of the Goleen. Off the island it is often covered with the tuberculous *Melobesia* mentioned in the previous section, in others by sponges, which grow to a considerable size and in which a hole, about the size of a five-shilling piece in diameter, is kept open by the scallop. In some cases the growth of *Melobesia* is so heavy that a similar state of affairs is brought about here too.

*Littorea littorea* (L.) and *Mytilus edulis* L. are present in even greater numbers, for, besides being very abundant in certain places, they are generally distributed wherever the substratum is suitable. Clumps of mussels occur in many places, such as the rocks in the Goleen, the rocky islet at the northern corner, and especially at the Sill in the Rapids. Some of these may be described as small reefs, and are clothed with *Tubularia*, *Plumularia*, other Hydrozoa, and Polyzoa, besides harbouring many errant forms, notably Ophiuroids and Polychaetes.

Of the remaining Gastropoda *Gibbula cineraria* (L.) and *G. umbilicata* (Mont.) are common and very generally distributed, though on account of its beauty and of the fact that it is much less usually met with, *Trivia europaea* (Mont.), the European cowrie, is more conspicuous than they are. This species occurs especially in the region of the Rapids, including Southern's Bay.

Of Opisthobranchs *Aplysia punctata* Cuv., the sea-hare, and *Oscanius membranaceus* (Mont.), occur occasionally, and *Pleurobranchus plumila* (Mont.) is moderately common. Nudibranchs are well represented, *Jorunna johnstoni* (A. and H.) being the most plentiful and showing very interesting colour variations, which render it very inconspicuous against the sponges on which it feeds. One particularly arresting case of this was met with during 1928, when a pairing couple was found, one individual of which was dark scarlet, the other dirty yellow, their colours matching exactly two adjacent sponges on which they were standing, and into which they had eaten. *Limapontia capitata*

(Müll.) and *Elysia viridis* (Mont.) occur in numbers, but so far *Alderia* has not been observed, though Lough Ine is but 4 miles from the original locality for this genus—in the River Ilan.

Nudibranchs and Tectibranchs constitute such a feature of the fauna of the shores of the Lough and of Southern's Bay that a list of species identified to date is of considerable interest:

## NUDIBRANCHS

*Archidoris tuberculata* (Cuv.)  
*A. testudinaria* (Risso.)  
*Jorunna johnstoni* (A. and H.)  
*Rostangia coccinea* (Forbes)  
*Doris flammea* (A. and H.)  
*Aegires punctilucens* (d'Orb.)  
*Triopa claviger* (O.F.M.)  
*Goniodoris castanea* (A. and H.)  
*G. nodosus* Mont.  
*Lamellidoris bilamellata* (L.)  
*Acanthodoris pilosa* (O.F.M.)  
*Ancula cristata* Alder  
*Doto pinnatifida* (Mont.)  
*Polycera quadrilineata* (O.F.M.)  
*P. ocellata*  
*Antiopella cristata* (delle Chiaje)

*Galvinia farrani* (A. and H.)  
*G. picta* A. and H.  
*G. tricolor* (Forbes)  
*Facelina drummondi*  
*F. punctata* (A. and H.)  
*F. coronata* (Forbes)  
*Tergipes despectus* (Johnst.)  
*Aeolidia papillosa* (L.)  
*Eolis angulata*  
*Pleurophyllidia loveni* Bergh.  
*Elysia viridis* Mont.  
*Limopontia capitata* Müll.

## TECTIBRANCHS

*Acera bullata* Müll.  
*Aplysia punctata* Cuv.  
*Oscanian membranaceus* (Mont.)  
*Pleurobranchus plumula* (Mont.)

As related in the introduction, Lough Ine was once frequented for the sake of its oysters. Now, however, *Ostraea* is scarce in the living state, though its former abundance is vouched for by the quantities of valves which persist, while there is still a very small bed below the main part of Southern's Bay<sup>1</sup>.

"Worms" belonging to very different groups are well represented, but by far the most plentiful species is the Serpulid *Pomatoceros triqueter* Morch., which in many places covers a considerable proportion of the surface of stones and rocks. This is especially the case in a little bay on the eastern shore of the Goleen, where the slabs are all but covered by the chalky tubes of this species, which here form a retreat for *Phoronis hippocerepea* L. This remarkable form occurs also in the thick encrusting Corallines found at the north-west point of Castle Island, and probably elsewhere. Polynoids, too, are abundant, but the most conspicuous worms, by reason of both their numbers and their large size, are the Terebellid *Polymnia nebulosa* (Mont.), which fortifies its sinuous slimy covering with small stones and fragments of shell, and the bright orange coloured Nemertinean *Cerebratulus marginatus* Renier, whose delicate membranous tube has the appearance of semi-translucent mica.

After *Paracentrotus* the most striking of the Echinodermata is *Asterias glacialis* L., small specimens, up to 5 or 6 inches in diameter being common on the under-surface of rocks and boulders along the shore, while large ones, up to 16 inches in diameter, are common in deep water. The difference in colour between the shore and off-shore specimens is very marked, a steely blue-grey prevailing in the former, various shades of yellowish brown in the latter.

<sup>1</sup> The upper part of Barloge Creek, where it broadens out on the west we designate Southern's Bay in acknowledgment of Mr T. C. Southern's work of 1915. See Plate XXIV, Phot. 8.

*Asterias rubens* L., the common cross-fish, is by no means common, and rarely reaches 4 inches in diameter. This predominance of *A. glacialis* and *Paracentrotus* furnishes us with a very salutary warning against the far too prevalent habit of referring to a species as "the common, or the usual so-and-so," for on most parts of the coasts of the British area *A. rubens* and *Echinus esculentus* are the common or usual species.

Ophiuroids (brittle stars) are represented chiefly by *Ophiothris fragilis* (O.F.M.) and *Ophiocoma nigra* (O.F.M.), the common and black brittle stars, both of which show wide ranges of colour variation, though several other species occur. *Echinus esculentus* L. is usually plentiful along the part of the eastern shore which faces the Rapids, and on the steep rocks opposite to this on the western shore. Southern records it as being abundant on the eastern shore of the Rapids, but we did not find it there at all until 1928, and then only in very small numbers. From the way in which it appears at, and disappears from, other places in the Lough this species appears to do a good deal of moving about. It occurs in large numbers on the steep rocks at the mouth of Barloge Creek, north of Carrigathorna. *Echinus miliaris* L. may be mentioned here, though it is anything but common, because it occurs in a few places where *Paracentrotus* is scarce, or from which it is absent. This species resembles *E. esculentus* in being abundant just outside the Lough, its favourite haunt being on the eastern side of the spit which separates Barloge Creek from Tranabo Cove at low water, and which is known as the Coosh.

Of Crustacea the most abundant of the larger forms are the porcelain crabs, *Porcellana platycheles* (Penn.) and *P. longicornis* (L.), both of which, the former especially, are very numerous on the under-surfaces of stones and in crevices containing stones, with smaller numbers of *Xantho incisus* (Leach) and *Pilumnus hirtellus* (L.). Young specimens of *Cancer pagurus* L. are common too, but *Carcinus maenas* (Penn.) is astonishingly uncommon, except in the Goleen, where a considerable proportion of their number is infested with the parasitic barnacle, *Sacculina carcini* (Thomp.). *Verruca stroemii* (O.F.M.) is by far the commonest barnacle, and occurs in large numbers on the under-surface of stones, especially those in crevices. The common acorn barnacle, *Balanus balanoides* (L.), is much less frequent, the largest specimens growing on the wall which forms the western boundary of the Rapids, a considerable percentage of them being parasitised by the Isopod, *Cryptothir balani*. Caprellids and other small Crustacea live in surprising numbers among the Hydroids of the mussel beds and of large stones in the Rapids.

Polyzoa, Tunicata, both simple and compound, and Porifera, are extremely abundant wherever there is a suitable substratum. The second of these are remarkable for their brilliancy of colour, especially in the Rapids and the regions most affected by the incoming tide. So great are the differences in both colour and conformation that it is difficult to subscribe to the view that there is but one species of *Botryllus*.



The Porifera are among the most interesting of the sessile inhabitants of both the Lough and Barloge Creek, being exceedingly numerous and exhibiting tremendous variation of both form and colour, *Hymeniacidon caruncula* Bwk., *Suberites carnosa* (Johnst.) and *Tethya lynceurium* (L.) affording three common examples. Brilliant blue patches of *Terpios fugax* Duch. and Mich., whose colour is due to a symbiotic Beggiotacean alga, are frequent, but more remarkable than any of these is the abundance of *Hymedesmia stevensi* Burton, a species but recently described by Burton from scanty material found at Plymouth<sup>1</sup>. A second new species, *Halichondria bowerbankia*, described in the same paper, also occurs in the Lough. The influence of light as a factor in the production of colour is well shown by masses of *Pachymatisma johnstoni* Bwk., which grow in a long narrow cave on the western side of Bullock Island. Near the mouth of the cave the outer parts, which are subjected to bright light are so dark that an ordinary observer would call them black. A little further in it becomes obvious that the "black" is really a very dark purple, and as we go farther and farther from the source of light the colour pales gradually until the sponge is almost white.

Abundant but "local" species of Coelenterata constitute striking features of the regions which they inhabit. Chief among these are *Cereus pedunculatus* (Pennant)<sup>2</sup>, which is so abundant right across the middle region of the Goleen, along the northern shore of the island from the middle round to the rocks at the eastern end, and in Southern's Bay, that it forms regular fields, in addition to filling crevices in the ridges just south of the quay in Barloge Creek; *Anemonia sulcata* (Penn.), found with *Cereus* in the second habitat mentioned above, and on *Zostera* in the Goleen, to the east of the Coosh, and abundantly in Southern's Bay; *Corynactis viridis* Allman, many varieties of which literally cover the undersurface of slabs, large and small in some regions, notably in and near to the Rapids: slabs which rest on one edge are often entirely covered except for the small area which touches their support; *Obelia geniculata* L. which clothes the fronds of *Laminaria digitata* Edm. and *L. saccharina* Lam. in most of the places where these occur; in many cases it is of quite a distinct red colour: *Sertularia operculata* L. which occurs in large quantities on slabs in the Rapids, where, as already mentioned, it is tenanted by hordes of *Caprellids* (and other Synca-rida). The other common Coelenterate which is very abundant at times is *Aurelia aurita* Lam. the common jellyfish. Of this there appear to be two "broods"—one from April to June, the other from July or August to late autumn. There is some evidence that the former is the outcome of strobilisation within the Lough, and that the latter is brought in on the flood tides, but this needs further investigation.

Three other species of Coelenterata, all fairly abundant, are worthy of

<sup>1</sup> Burton, "Additions to the Sponge Fauna at Plymouth." *J. Mar. Biol. Ass. N.S.* xvi, 2. March, 1930.

<sup>2</sup> Probably other species are included here, too.



special mention. These are the so-called cup-coral, *Caryophyllia smithii* Stokes, which careful searching has shown to be anything but scarce in places which afford a roof-like habitat just below the limit of low water at spring tides in the Creek and of neap tides in the Lough; *Sarcodictyon catenata* Forbes, which is less common but by no means rare; and a new species of Alcyonarian, closely related to but differing in several important features from *Parerythropodium norvegicum* Kor. and Dan., for which the name *P. hibernicum* has been suggested. There is just the possibility that this may be the adult stage of *Harteia elegans*, described by Wright in 1864<sup>1</sup>, from a single specimen found attached to a shell in deep water off the west coast of Ireland. Unfortunately Wright's description and figure are not detailed enough to enable a proper comparison to be made between this form and the earliest single-polyte stage of the new species.

All the species to which reference has been made above are to be obtained by shore-collecting, the majority of them either exposed or in water of but a few inches in depth during the periods of low tide, and it is of especial interest that a number of them, such as *Echinus esculentus*, *Ophiothrix fragilis*, *Ophiocoma nigra*, *Asterias glacialis*, and *Caryophyllia smithii* are usually obtainable only by means of a dredge. To this list must be added the Brachiopod *Crania anomala* Müll., the Crinoid *Antedon bifida* (Penn.), the Lamellibranch *Lima hiens* (Gm.), and the Polychaete *Chaetopterus variepedatus* Ren., while but one littoral form, other than *Alcyonium*, closely related to *P. hibernicum* is known.

To this general description may be added an account of a specific region, as an example of what the shore of the Lough is like. For this purpose the part of the southern shore, S. 12 to S. 17 on Map III is taken.

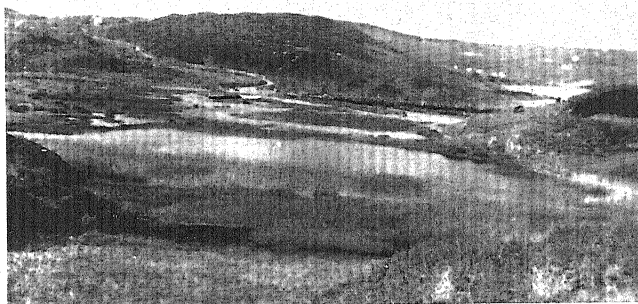
S. 12 is a small ridge of rocks: S. 13, Scyllium Bay, has been formed through the breaking down of the rocks, and consists at low water of a horseshoe-shaped strand, backed by a flat sward, at the foot of which are large blocks of rock. The floor is of coarse muddy sand and stones, and at spring tides, a wide area of small boulders clothed with algae, conspicuous among which are *Cystoseira ericoides* Ag. and *Lithophyllum lichenoides* Ellis. S. 14 is another ridge, some 10 feet high and practically sheer along its eastern half. This wall of rock continues round to the Narrows, but is broken up into jutting ridges, which form little bays at S. 16 and S. 17. At S. 15 and S. 16 are zones of boulders and small slabs on a gently sloping bottom, separated from each other by a large rock. S. 16 bears a small field of *Cystoseira*. S. 17 is very rugged and slopes down from a narrow boulder zone into deep water very rapidly. It is subjected to the full influence of tides flooding into and ebbing from the Lough.

The narrow land region between S. 13 and S. 17 consists of a high ridge of rocks, marked by Gorse and Heather. The laboratories are situated on the sward above Scyllium Bay and behind the ridge near S. 17 (Plates XXIV, XXV, Photos. 8, 11).

<sup>1</sup> Wright, P., on a new genus of Alcyonidae (*Harteia elegans*). *Proc. Dub. Micro. Club*, 1864.



Phot. 11. Lough Ine. The laboratories at Scyllium Bay and the Rapids.



Phot. 12. Tralispean Marsh. The Bealariree Stream enters from the left. Tragemona Bay in the right distance.



Phot. 13. Tragemona Strand at low water. The lake is just to the right of the school house.

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The shore area from which the following species have been identified is approximately 235 yards in length and averages 4 yards in width.

## LOUGH INE. S. 12—S. 17.

## PORIFERA

*Clathrina coriacea* (Mont.)  
*C. contorta* (Bwk.)  
*Leucosolenia botryoides* (Ellis and Sol.)  
*Sycon ciliatum* (Fabr.)  
*S. raphanus* Schmidt  
*Leucandra nivea* (Grant)  
*Halisarca dujardini* Johnston  
*Pachymatisma johnstoni* (Bwk.)  
*Tethya lyncurium* (L.)  
*Cliona celata* Grant  
*Terpios fugax* Duch. and Mich.  
*Reniera cinerea* (Grant)  
*Halichondria panicea* (Pallas)  
*H. Bowerbankia* Burton  
*Hymedesmia stevensi* Burton  
*Myxilla incrustans* (Johnst.)  
*M. contrarenii* (Martens)  
*Esperiopsis fucorum* (Johnst.)  
*Hymeniacidon sanguineum* (Grant)  
*Aplysilla rosea* Schultze  
*Plakina monolopha*

## COELENTERATA

## GYMNOBLASTEA

*Clava muticornis* Forshal.  
*C. squamata* (Müller)  
*Tubularia bellis* Allman

## CALYPTOBLASTEA

*Obelia geniculata* (L.)  
*Campanularia flexuosa* (Hincks)  
*C. neglecta* (Alder.)  
*Sertularia pumila* L.  
*S. operculata* L.

## DISCOMEDUSAE

*Aurelia aurita* (L.)

## ANTHOZOA

## ALCYONARIA

*Acyonium digitatum* L.  
*Parerythropodium hibernicum* sp. nov.  
*Sarcodictyon catenata* Forbes

## ZOANTHARIA

*Actinia equina* Linn. var. *fragacea*  
*Metridium senile* (L.)  
*Anemonia sulcata* (Penn.)  
*Bunodactis verrucosa* (Penn.)  
*Anthopleura ballii* (Cocks)  
*Corynactis viridis* Allman

## MADREPORARIA

*Caryophyllia smithii* Stokes

## CTENOPHORA

*Pleurobrachia pileus* Fabricius

## ECHINODERMATA

## HOLOTHUROIDEA

*Cucumaria saxicola* Brady and Robertson

## CRINOIDEA

*Antedon bifida* (Penn.)

## ASTEROIDEA

*Asterina gibbosa* (Penn.)  
*Asterias rubens* L.  
*A. glacialis* L.

## OPHUROIDEA

*Amphiura elegans* (Leach)  
*Ophiocoma nigra* (Abild.)  
*Ophiorthrix fragilis* (Abild.)

## ECHINOIDEA

*Echinus miliaris* Gmel.  
*E. esculentus* L.  
*Paracentrotus lividus* (Lmk.)

## TURBELLARIA

*Leptoplana tremellaris* (Müller)  
*L. fallax* (Quatrf.)  
*Prostheceraeus vittatus* (Mont.)

## NEMERTINEA

*Lineus longissimus* Gunn  
*Cerebratulus marginatus* Renier

## ANNELIDA

## ARCHIANNELIDA

*Dinophilus taeniatus* Harmer

## POLYCHAETA

*Euphrosyne foliosa* Aud. and Edw.  
*Lepidonotus squamatus* (L.)  
*L. clava* (Montagu)  
*Lagisca floccosa* (Sav.)  
*Harmothoe imbricata* (L.)  
*Halosydna gelatinosa* (M. Sars.)  
*Sthlenelais boa* (Johnst.)  
*Eulalia viridis* (Müller)  
*Nereis pelagica* L.  
*Staurocephalus rubrovittatus* Grube  
*Lysidice ninetta* Aud. and Edw.  
*Cirratulus cirratus* (O.F.M.)  
*Polymnia nebulosa* (Mont.)  
*Stylariodes plumosa* (O.F.M.)  
*Flabelligera affinis* Sars.  
*Pomatoceros triquetus* L.  
*Spirorbis spirorbis* (L.)

## GEPHYREA

*Phascolosoma johnstoni* (Forbes)

## POLYZOA

*Pedicellina cernua* Pallas  
*Crisia eburnea* L.  
*C. cornuta* L.  
*Diastopora patina* Lmk.  
*Lichenopora hispida* Fleming  
*Euratea chelata* L.  
*Bugula calathus* Norman  
*B. flabellata*  
*Scrupocellaria reptans* L.

Membranipora membranacea L.  
 Electra pilosa L.  
 Electra pilosa var. dentata Ellis and Solander  
 Smithia landsborovii Johnston  
 Aleyonidium mytili Dalyell  
 Flustrella hispida Fabricius  
 Bowerbankia imbricata Adams var. densa Farre

## BRACHIOPODA

Crania anomala Müller

## ARTHROPODA

## CRUSTACEA

## ENTOMOSTRACA

Ascidicola rosea Threll.  
 Verruca stroemia Müller  
 Balanus balanoides L.  
 B. porcatus da Costa

## ARTHROSTRACA

Tanais cavolini M. Ed.  
 Ligia oceanica (L.)  
 Naesa bidentata (Adams)  
 Jaera marina (Fabr.)  
 Janira maculosa Leach  
 Gammarus marinus Leach  
 Amphithoe rubricata (Mont.)  
 Microdeutopus anomalus (Rathke)  
 Jassa dentex (Czerniavski)  
 Parajassa pelagica (Leach)  
 Caprella acanthifera Leach

## DECAPODA

Cancer pagurus L.  
 Pilumnus hirtellus (L.)  
 Xantho incisus (Leach)  
 Carcinus maenas (Pennant)  
 Inachus dorsettensis (Pennant)  
 Portunus puber (L.)  
 P. arcuatus Leach  
 Porcellana longicornis (L.)  
 P. platycheles (Pennant)  
 Galathea squamifera Leach  
 Hippolyte varians Leach  
 Spirontocaris eranchi (Leach)  
 Leander serratus (Pennant)  
 L. squilla (L.)

## INSECTA

Anura maritima Laboulb.  
 Machilis maritima Leach

## MYRIAPODA

Scolioplanes maritima (Leach)

## PYCNOGONIDA

Pycnogonum littorale Stroem  
 Nymphon rubrum Hodge

## MOLLUSCA

## AMPHINEURA

Acanthochites fascicularis (L.)  
 Craspedochilus cinereus (L.)

## PELECYPODA

Anomia ehippium L.  
 Anomia ehippium var. striatum

Mytilus edulis L.  
 Volsella modiolus (L.)  
 V. phaseolina (Phil.)  
 Modiolaria marmorata (Forbes)  
 M. discors (L.)  
 Pecten varius (L.)  
 Kellia suborbicularis (Mont.)  
 Tapes decussatus (L.)  
 Venus verrucosa L.  
 Cardium exiguum Gmel.  
 C. edule (L.)  
 Saxicava rugosa L.  
 Ostrea edulis (L.)

## GASTROPODA

Patella vulgata (L.)  
 Helcion pellucidum (L.)  
 Acmacea virginea (Müll.)  
 Emarginula fissura (L.)  
 Fissurella graeca (L.)  
 Gibbula umbilicata (Mont.)  
 Calliostoma zizyphinus (L.)  
 Phasianella pullus (L.)  
 Littorina obtusata (L.)  
 L. rudis (Maton)  
 L. littorea (L.)  
 Rissoa parva (da Costa)  
 Rissoa parva var. interrupta  
 R. proxima Alder  
 R. violacea Desmarest  
 Cingula semistriata (Mont.)  
 Trivia europaea (Mont.)  
 Bittium reticulatum (da Costa)  
 Ocinebra erinacea (L.)  
 Purpura lapillus (L.)  
 Nassa incrassata (Stroem)

## TECTIBRANCHIATA

Pleurobranchus plumula (Mont.)  
 Oscanus membranaceus (Mont.)

## NUDIBRANCHIATA

Archidoris tuberculata (Cuv.)  
 A. testudinaria (Risso)  
 Jorunna johnstoni (A. and E.)  
 Rostangia coccinea (Forbes)  
 Aegires punctilucens (d'Orb)  
 Triopa clavigera (O.F.M.)  
 Lamellidoris bilamellata (L.)  
 Goniodoris castanea (A. and H.)  
 Ancula cristata Alder  
 Doto pinnatifida (Mont.)  
 Galvania farrani A. and H.  
 G. picta (A. and H.)  
 G. tricolor (Forbes)  
 Facelina punctata A. and H.  
 Cuthona peachi (A. and H.)  
 Tergipes despectus (Johnst.)  
 Aeolidia papillosa (L.)  
 Pleurophyllidia loveni Bergh.  
 Limopontia capitata Müller  
 Elysia viridis Mont.

## TUNICATA

Phallusia mentula (Müll.) = Ascidia rubicunda Hanc.  
 P. virginea (Müll.)  
 Ascidia aspersa (Müll.)  
 Ciona sociabilis (Gunn) = C. intestinalis (L.)

*Ascidia producta* Nanc.  
*Styela rustica* L.  
*Cynthia squamulosa* A. and H.  
*Clavelina lepadiformis* (Müll.)  
*Aplidium zostericola* (Giard)  
*Amouricium proliferum* M.E.  
*Dendrodoa grossularia* (Bened.)  
*Parascidia flemingii* A. and H.  
*Didemnum durum* M.E.  
*Leptoclinum gelatinosum* (M.E.)  
*L. fulgens* (M.E.)  
*L. griseum* A. and H.  
*L. maculosum* A. and H.  
*Botryllus schlosseri* (Pallas)  
*Botrylloides rubrum* M.E.

## PISCES

*Scyllium canicula* (L.) and "purses"  
*Conger vulgaris* Cuv.  
*Anguilla vulgaris* Turton  
*Gobius rithensparri* Euphras.  
*G. minutus* (L.)  
*Cottus bubalis* Euphras.  
*Liparis montagui* (Donovan)  
*Lepadogaster gouani* (Lacep.)  
*Blennius pholis* (L.)

## PHANEROGAMIA

*Ranunculus ficaria* L.  
*R. repens* L.  
*Cochlearia danica* L.  
*C. officinalis* L.  
*Viola* (canina)  
*Polygala vulgaris* L.  
*Cerastium viscosum* L.  
*Spergularia marina* L.  
*Ilex aquifolium* L.  
*Ulex europaeus* L.  
*Anthyllis vulneraria* L.  
*Lotus corniculatus* L. var. *crassifolius* Pers.  
*Lathyrus pratensis* L.  
*Rubus fruticosus* L.  
*Prunus spinosa* L.  
*Sedum anglicum* Huds.  
*Hedera helix* L.  
*Lonicera periclymenum* L.  
*Scabiosa succisa* L.  
*Hieracium pilosella* L.  
*Bellis perennis* L.  
*Matricaria inodora* L. var. *maritima* L.  
*Hypochaeris radicata* L.  
*Taraxacum officinale*  
*Achillea millefolium* L.  
*Vaccinium myrtillus* L.  
*Erica cinerea* L.  
*Calluna vulgaris* L.  
*Statice maritima* Mill.  
*Primula vulgaris* Huds.  
*Glaux maritima* L.  
*Plantago lanceolata* L.  
*P. coronopus* L.  
*P. maritima* L.  
*Digitalis purpurea* L.  
*Euphrasia officinalis* L.  
*Thymus serpyllum* L.  
*Teucrium scorodonia* L.  
*Atriplex rosea* L.  
*Suaeda maritima* Dum. procumbens Syme

*Euphorbia hiberna* L.  
*Juncus maritimus* Lam.  
*Luzula sylvatica* Gaud.

## PTERIDOPHYTA

*Pteris aquilina* L.

## BRYOPHYTA

## MUSCI

Some

## HEPATICAE

*Frullania germana* Taylor

## THALLOPHYTA

## LICHENES

*Lichina pygmaea* Ag.  
*Ramalina scopulorum* Ach.  
 (R. *calicaris* Hiffm.)  
*Usnea hirta* Hoffm.  
*Parmelia perlata* Ach.  
*Xanthoria parietina* Ach.  
*Physcia aquilina* Ach.  
*P. stellaris* Ach.  
*Lecanora murorum* Ach.  
*L. atra* Ach.  
*L. tartarea* Ach.  
*Cladonia pyxidata* Fr.  
*C. furcata* Ach.  
 (C. *cervicornis*)  
*Lecidea contigua* Fr.  
*L. elaeochroma* Ach.  
*Verrucaria maura* Wahlenb.  
*V. mucosa* Wahlenb.

## ALGAE

## CYANOPHYCEAE

*Rivularia atra* Roth.  
*Microcoleus anguiformis* Harv.  
*Calothrix semiplena* Ag.

## CHLOROPHYCEAE

*Ulva latissima* L.  
*Enteromorpha intestinalis* Link  
*E. compressa* Grev.  
*Cladophora rupestris* Kg.  
*C. hutchinsiae* Harv.  
*C. flexuosa* Griff.

## PHAEOPHYCEAE

*Asperococcus bullosus* Lamour.  
*A. echinatus* Grev.  
*Ectocarpus granulosus*  
*Pylaiella littoralis* Kjellm.  
*Elachista fucicola* Fries  
*Ralfsia* sp.  
*Mesogloia griffithsiana* Grev.  
*M. vermicularis* Ag.  
*Leathesia tuberosa* S.F.G.  
*Chorda filum* Stackh.  
*Laminaria saccharina* Lamour.  
*Laminaria saccharina* var. *phyllitis* Le Jol.  
*Fucus spiralis* L.  
*F. vesiculosus* L.  
*F. serratus* L.  
*Ascophyllum nodosum* Le Jol.  
*Pelvetia canaliculata* Decne. et Thur.  
*Himanthalia lorea* Lyngb.  
*Cystoseira ericoides* Ag.



## RHODOPHYCEAE

*Gelidium corneum* Lamour. var. *K. abnorme* Grev.

*Chondrus crispus* Lyngb.

*Gigartina mamillosa* Ag.

*Rhodomenia bifida* Grev.

*R. laciniata* Grev.

*R. laciniata* very narrow

*Chylocladia kaliformis* Hook.

*Delessaria hypoglossum* Ag.

*Laurencia pinnatifida* Lamour.

*Laurencia pinnatifida* var. *littoralis*

*Laurencia pinnatifida* var. *angusta*

*Polysiphonia elongata* Grev.

*P. fastigiata* Grev.

*Callithamnion roseum* Lyngb.

*C. virgulatum* Harv.

*C. affine* Harv.

*C. pedicellatum* Ag.

*C. brachiatum* Bonnem

*Ceramium diaphanum* Roth.

*C. rubrum* Ag.

*C. echionotum* Ag.

*Dumontia filiformis* Grev.

*Dilsea edulis* Stackh.

*Hildenbrandtia* Sp.

*Melobesia pustulata* Lamour.

*Lithophyllum lichenoides* Ellis

*Corallina officinalis* L.

*Dredging, etc.* Dredging in the Lough itself is rather disappointing, mainly because the amount of hard ground is so small and the area of mud so large. The most abundant forms dredged are "worms," including Polychaetes, Nemertineans and Nematodes; Molluscs, the chief of which are *Acera bullata* Müll. and *Philine aperta* (L.), the former with spawn, and *Turritella communis* Lmk.; Crustacea, chiefly the swimming crabs, *Portunus arcuatus* Leach, and *P. corrugatus* (Penn.), rarely hermit crabs, the largest *Eupagurus bernhardus* (Lin.) occurring in shells of *Gibbula magus* (L.), a few *E. prideauxii* (Leach) with poor specimens of *Adamsia palliata* (Bod.), the cloaklet anemone, and *E. cuanensis* (Thomp.), on one of which was the parasitic Isopod *Athelges* sp. *Calocaris macandreae* Bell, a single specimen, and numerous Amphipods; and the Echinoderms *Amphiura chiajii* Forbes, and *Asterias glacialis* L. large specimens.

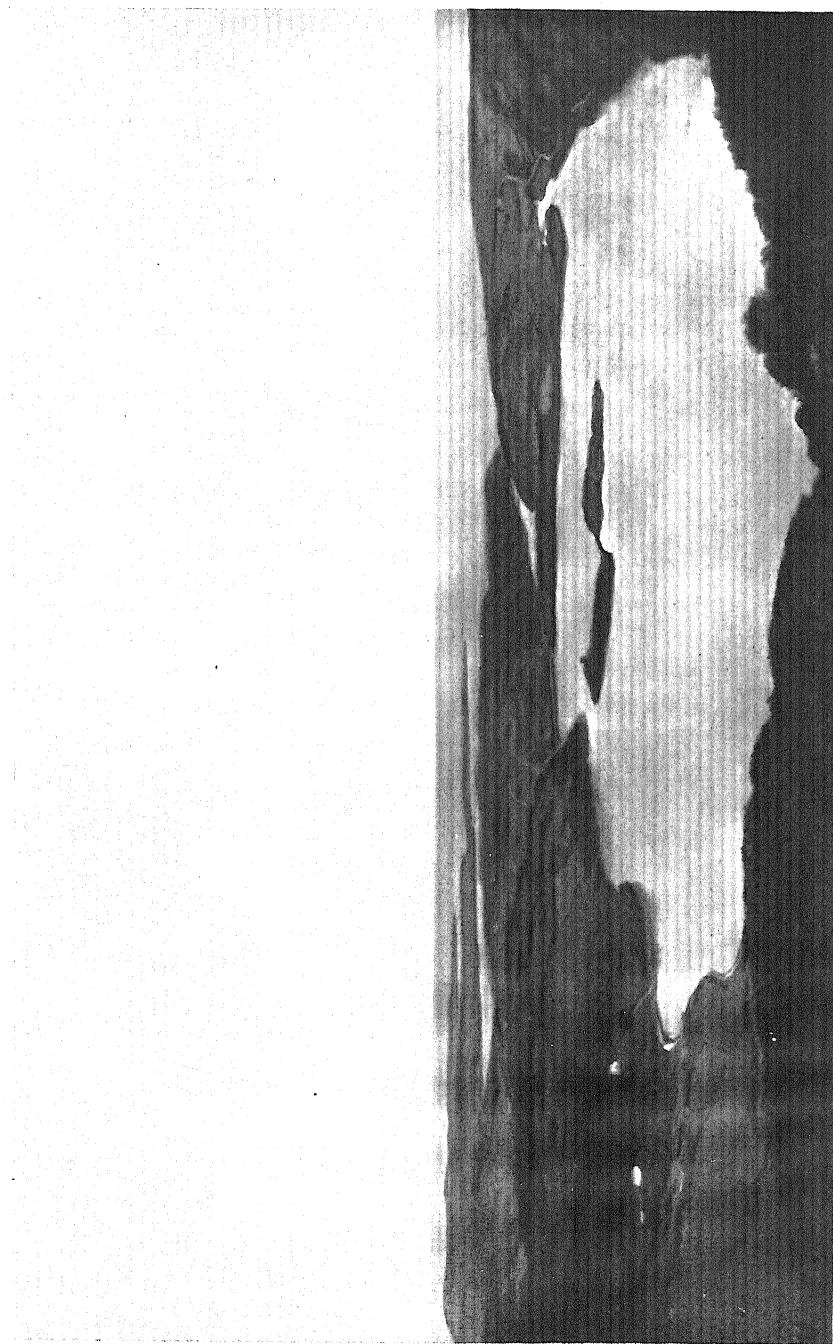
In the southern half of Barloge Creek a greater variety of the larger forms are taken by the dredge, including large numbers of spider crabs of different kinds, an occasional *Eledone cirrhosa* Lmk. and various fish (see list later).

Experiments have proved that a good deal of the bottom is suitable ground on which to use Mortensen's method of bottom tow-netting, and surface tow-netting is carried on as regularly as possible from a boom which is slung out over the Rapids at half-flood and half-ebb tides. None of the samples taken have yet been properly examined.

At times currents from the Atlantic result in additions to the more normal inhabitants of the Creek and the Lough. In this way *Veella spirans* Lam., *Pelagia perla* (Slabber) and *Aequorea forskalea* Peron and Les., have been brought in in small shoals, as also small numbers of *Lepas pectinata* Spengler, one specimen (dead) of *Chelone imbricata* and a cocoa-nut both with colonies of *Lepas anatifera* L. of the same size growing on them; and a packet of love letters, which appears to have been cast overboard from an American vessel.

*Barloge.* The small peninsula which constitutes the holding of Barloge, consists of rocky heather-gorse moorland, rising to over a 100 feet on the east, but with some good fields on the west and north. The largest fertile area slopes down towards the Goleen, from which its northernmost portion is flooded at high spring tides. As a result of this it bears a characteristic flora of *Spergularia*, *Cochlearia* (which bears a few mauve flowers), *Triglochin*, *Plantago*,





Phot. 14. Lough Ine from the north: the Goleen to the right.

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*Salicornia*, and *Atriplex*. At the end of September, 1930, a large part of this region had the appearance of having been sprinkled with coarse salt. Examination determined this to be due to countless larvae of a Coccid, belonging to the genus *Orthezia*. These were still abundant in December, and some of them kept in the laboratory at University College, Cork, are still alive, so it is hoped that they will complete their development<sup>1</sup>.

The little islets in the Goleen are all submerged during high spring tides, and are being gradually washed away. Their flora is composed chiefly of grasses and rushes, among which the species mentioned just above are scattered. Small puddles left by the tide bear the miniature varieties of Fuci on their edges. In these puddles and on the flood land with the *Orthezia Salda pallipes* F. abounds.

The uncultivated land includes two small areas of marsh, one of which is permanently under water.

*Bellis perennis* L. with variegated leaves occurs in places. In the experience of the author such variegated plants do not bear flowers. (They occur also in part of the grounds of University College, Cork. Out of Ireland they have been met with in the island of Cumbræ, in the Firth of Clyde.) Many parts of the peninsula provide ideal conditions for the very beautiful Irish spurge, *Euphorbia hiberna* L., which takes full advantage of them. This plant occurs all through the district under consideration, but is seen at its best in this particular locality. The general flora is very varied, partly on account of the physical differences between parts of the holding, partly because it has been inhabited for many centuries, as is testified by the presence of ancient erections, Druidical, early Irish, and early Christian, and some possibly from even earlier times. These relics of the past include alignments, standing stones, a liss or ancient fort, a church, and incised grave stones. *Anthoceros* sp. occurs in quantity a short distance away from the homestead of Barloge.

*Castle Island* (Plate XXVI, Phot. 14). At high water of spring tides this is divided into two, through the flooding of the low strand of gravel and small rocks which separates the loftier eastern from the lower western half. The physical features of the two halves are so different that there is very little in common between the biological associations which characterise them. These last are being worked out in full. The Coralline region off the north shore has been mentioned in the general part.

*Barloge Creek*. Including the Narrows the Creek is about two-thirds of a mile long. The Narrows are a little over 100 yards in length, but are only 30 feet wide at low water; small though they are their importance from the biological aspect cannot be exaggerated, on account of the effects they produce in both the Lough and the Creek. The channels in the Creek are very narrow owing to the presence of banks of *Zostera*, whilst forests of *Chorda filum* Stackh. make navigation even more difficult during the summer. Southern's Bay, which constitutes the widest part of the Creek, is a favourite collecting ground

<sup>1</sup> Since this was written adults, abundant during June, show this to be *Orthezia urticae* (Lin.).

with visiting classes. The narrow southern end supports great quantities of Algae, which show zoning very distinctly, and large numbers of *Echinus esculentus* L. Two of the most interesting records from this region are of *Holothuria forskali* Delle Chiaje, an Echinoderm usually obtained by dredging, and the Chelifer *Obisium maritimum* Leach, whose habits are comparable with those of *Aepus*.

At high water, when Bullock Island is separated from the mainland, Barloge Creek communicates with Tranabo Cove, but at low water Bullock is reached from the mainland across a strand, the Coosh, a short account of which follows later. The cave, in which the effects of light on *Pachymatisma* are so clearly demonstrated, penetrates the western side of Bullock Island, a few yards north of the open sea.

Short hauls with the dredge have been made as opportunity allowed, and the animals taken, in addition to *Zostera* and Algae, are summarised in the following list, which bears a striking contrast with that for Tragemona, which follows later.

#### DREDGING BARLOGE CREEK.

- |  |   |
|--|---|
| <b>PORIFERA</b>                        | <i>Inachus dorynchus</i> Leach                |
| <i>Hymeniacidon sanguineum</i> (Grant) | <i>Stenorhynchus rostratus</i> L.             |
| <b>COELENTERATA</b>                    | <i>Ebalia</i> sp. carapace                    |
| <i>Anthopleura ballii</i> (Cocks)      | <i>Portunus puber</i> (L.)                    |
| <b>ECHINODERMATA</b>                   | <i>P. depurator</i> (L.)                      |
| <b>ASTEROIDEA</b>                      | <i>P. arcuatus</i> Leach                      |
| <i>Asterias rubens</i> L.              | <i>Porcellana longicornis</i> (L.)            |
| <b>OPHIUROIDEA</b>                     | <i>P. platycheles</i> (Penn.)                 |
| <i>Ophiura albida</i> Forbes           | <i>Eupagurus bernhardus</i> (L.)              |
| <i>Ophiothrix fragilis</i> (Abild.)    | <i>E. prideauxii</i> (Leach)                  |
| <b>ECHINOIDEA</b>                      | <i>E. cuanensis</i> (W. Thompson)             |
| <i>Echinus esculentus</i> L.           | <i>Anapagurus laevis</i> (W. Thompson)        |
| <b>NEMERTINEA</b>                      | <i>Hippolyte varians</i> Leach                |
| <i>Lineus longissimus</i> (Gunn)       | <i>Crangon vulgaris</i> L.                    |
| <b>ANNELIDA</b>                        | <b>PYCNOGONIDA</b>                            |
| <i>Harmothoe imbricata</i> (L.)        | <i>Nymphon rubrum</i> Hodge                   |
| <i>Nereis pelagica</i> L.              | <b>MOLLUSCA</b>                               |
| <i>N. diversicolor</i> O.F.M.          | <b>PELECYPODA</b>                             |
| <i>Pomatoceros triqueter</i> (L.)      | <i>Pecten maximus</i> L.                      |
| <i>Filigrana inplexa</i> Berkeley      | <i>Dosinia lupulina</i> valves                |
| etc. and others not identified         | <i>Cardium nodosum</i> Turton                 |
| <b>CRUSTACEA</b>                       | <i>Gari ferroensis</i> (Chemnitz) fresh shell |
| <b>ENTOMOSTRACA</b>                    | <b>GASTROPODA</b>                             |
| <i>Peltogaster</i> sp.                 | <i>Gibbula cineraria</i> (L.)                 |
| <b>ARTHROSTRACA</b>                    | <i>G. miliare</i> (Brocchi)                   |
| <i>Idotea baltica</i> (Pallas)         | <i>Phasianella pullus</i> (L.)                |
| <i>L. linearis</i> (Penn.)             | <i>Bittium reticulatum</i> (da Costa)         |
| <b>DECAPODA</b>                        | <i>Trivia europaea</i> (Mont.)                |
| <i>Carcinus maenas</i> (Penn.)         | <i>Natica alderi</i> Forbes                   |
| <i>Pilumnus hirtellus</i> (L.)         | <i>Nassa incrassata</i> (Stroem)              |
| <i>Maia squinado</i> (Herbst.)         | <b>TECTIBRANCHIATA</b>                        |
| <i>Achaeus cranchii</i> Leach          | <i>Aplysia punctata</i> Cuv.                  |
|  | <i>Philine aperta</i> (L.)                    |
|  | <b>CEPHALOPODA</b>                            |
|  | <i>Eledone cirrhosa</i> (Lmk.)                |
|  | <i>Sepia officinalis</i> L. spawn             |



## PISCES

*Raia batis* L.  
*Nerophis lumbriciformis* (Yarrell)  
*Syngnathus acus* L.  
*Zeugopterus punctatus* (Bloch)

*Gobius ruthensparri* Euphras.  
*Cottus scorpio* (L.)  
*Callionymus lyra* L.  
*Centronotus gunnellus* L.

*The Coosh.* This consists of a bank of gravel and large stones fringed with boulders (Plate XXIV, Phot. 10), and built between crests of rock from the mainland and from Bullock. It is exposed only at low water. Its name and the rocky crests together point to its origin, the probable derivation of Coosh being from cuavas (pronounced cuash), which means stepping stones, all of which, except the crests, have become buried under the cargo of stones dropped by the waves, when they come round from each side of Bullock and meet.

At low water of spring tides an expanse of sand with small meadows of *Zostera* is exposed below the boulder zone along the eastern side of the Coosh, together with small areas of weed-covered boulders at the foot of the ridges of rock, which form the northern and southern boundaries. Examination of this region is not yet complete, but the fauna and flora are in such striking contrast to those of any region of Lough Ine itself that lists are appended for comparison with those given from the southern shore of the latter.

## THE COOSH, EASTERN SIDE.

## PORIFERA

*Clathrina coriacea* (Mont.)  
*Leucosolenia botryoides* (E. and S.)  
*Leucandra nivea* (Grant)  
*Sycon ciliatum* (Fabr.)  
*S. raphanus* Schmidt  
*Terpios fugax* Duch. and Mich.  
*Halichondria panicea* (Pallas)

## COELENTERATA

## HYDROMEDUSAE

## GYMNOBLASTEA

*Coryne pusilla* Gaertner

## CALYPTOBLASTEA

*Campanularia neglecta* (Alder.)  
*Sertularia pumila* L.

## SIPHONOPHORA

*Velella spirans* (Förskal)

## DISCOMEDUSAE

*Aurelia aurita* (L.)  
*Pelagia perla* (Slabber)  
*Cyanea capillata* Peron.  
*Aequorea forskalea* Peron. et Lea  
*Halielystus auricula* (Fabr.)  
*Lucernaria campanulata* Lamour.

## ANTHOZOA

## ZOANTHARIA

*Actinia equina* L. and var. *Fragacea*  
*Anemonia sulcata* (Pennant)  
*Sagartia troglodytes* Johnst.

## ECHINODERMATA

## ASTEROIDEA

*Asterias rubens* L.  
*Asterina gibbosa* (Pennant)

## OPHIUROIDEA

*Amphiura elegans* (Leach)  
*Ophiothrix fragilis* (Abild.)

## NEMERTINEA

*Lineus longissimus* (Gunn)

## ANNELIDA

## POLYCHAETA

*Euprosyne foliosa* Aud. and Edw.  
*Lepidonotus squamatus* (L.)  
*L. clava* (Montagu)  
*Lagisca floccosa* (Savigny)  
*Harmothoe imbricata* (L.)  
*Sthlenelais boa* (Johnst.)  
*Nereis pelagica* L.  
*N. diversicolor* O.F.M.  
*Glycera alba* Rathk.  
*Eulalia viridis* (Müller)  
*Eulalia viridis* var. *aurea* (Müller)  
*Cirratulus cirratus* (O.F.M.)  
*Dodecaceria concharum* Oersted  
*Amphitrite gracilis* (Grube)  
*Pomatoceros triquetus* (L.)  
*Spirorbis borealis* L.

## GEPHYREA

*Physcosoma granulatum* (Leuckart)  
*Thalassema neptuni* Gaertner



**POLYZOA**

*Lichenopora hispida* Fleming  
*Scrupocellaria reptans* L.  
*Membranipora pilosa* L.  
*Lepralia pallasiana* Moll.  
 etc.

**ARTHROPODA****CRUSTACEA****ENTOMOSTRACA**

*Balanus balanoides* L.  
*Verruca stroemi* Müller

**ARTHROSTRACA**

*Ligia oceanica* (L.)  
*Idotea baltica* (Pallas)  
*Gammarus marinus* Leach  
*Amphithoë rubricata* (Mont.)

**DECAPODA**

*Cancer pagurus* L.  
*Pilumnus hirtellus* (L.)  
*Xantho incisus* (Leach)  
*X. hydrophilus* (Herbst.)  
*Carcinus maenas* (Pennant)  
*Hyas araneus* (L.)  
*Inachus dorynchus*  
*Portunus puber* (L.)  
*Porcellana longicornis* (L.)  
*Porcellana platycheles* (Pennant)  
*Galathea squamifera* Leach  
*Eupagurus bernhardus* (L.)  
*Leander serratus* (Pennant)

**INSECTA**

*Anura maritima* Laboulb.  
*Machilis maritima* Leach  
*Aëpus robinii* Laboulb.  
*Aëpophilus bonnairei* Sig.

**PYCNOGONIDA**

*Pycnogonum littorale* Stroem  
*Nymphon rubrum* Hodge

**MOLLUSCA****AMPHINEURA**

*Acanthochites fascicularis* L.

**PELECYPODA**

*Anomia ehippium* L.  
*Modiolaria discors* (L.)  
*Pecten varius* L.  
*Saxicava rugosa* L.  
*Kellia suborbicularis* (Mont.)  
*K. minuta*

**GASTROPODA**

*Patella vulgata* (L.)  
*Helcion pellucidum* (L.)  
*Acmacea virginea* (Müller)  
*Emarginula fissura* (L.)  
*Gibbula umbilicata* (Mont.)  
*G. cineraria* (L.)  
*Calliostoma zizyphinus* (L.)  
*Phasianella pullus* (L.)  
*Littorina obtusata* (L.)  
*L. rudis* (Maton)  
*L. littorea* (L.)

*Rissoa proxima* Alder.  
*Trivia europaea* (Mont.)  
*Purpura lapillus* (L.)  
*Ocenebra erinacea* (L.)  
*Nassa incrassata* (Stroem)

**TECTIBRANCHIATA**

*Aplysia punctata* Cuv.  
*Pleurobranchus plumula* (Mont.)

**NUDIBRANCHIATA**

*Jorunna johnstoni* (A. and H.)  
 etc.

**TUNICATA**

*Ascidia producta* Hanc.  
*Clavellina lepadiformis* (Müller)  
*Botryllus schlosseri* (Pallas)

**PISCES**

*Motella tricirrata* Bloch.  
*Centronotus gunnellus* (L.)

**ALGAE****CYANOPHYCEAE**

*Lyngbya? flacca* Harv. on *Gelidium*

**CHLOROPHYCEAE**

*Conferva* sp.  
*Ulva latissima* L.  
*U. lactuca* L.  
*Enteromorpha intestinalis* Link  
*E. linkiana* Grev.  
*Cladophora rupestris* Kg.  
*C. flexuosa* Griff.  
*C. albida* Kütz  
*C. lanosa* Kütz  
*Codium tomentosum* Stackh.

**PHAEOPHYCEAE**

*Punctaria latifolia* Grev.  
*Asperococcus echinatus* Grev.  
*Ectocarpus siliculosus* Lyngb.  
*Pylaiella litoralis* Kjellm.  
*Cladostephus spongiosus* Ag.  
*Rytiplaea fruticulosa* Harv.  
*Leathesia tuberiformis* S.F.G.  
*Laminaria saccharina* Lamour.  
*Fucus spiralis* L.  
*F. vesiculosus* L.  
*F. serratus* L.  
*Ascophyllum nodosum* Le Jol.  
*Pelvetia canaliculata* Deene, et Thur.  
*Himanthalia lorea* Lyngb.  
*Cystoseira ericoides* Ag.

**RHODOPHYCEAE**

*Gelidium corneum* Lamour.  
*Gelidium corneum* var. *flexuosum*  
*Chondrus crispus* Lyngb. normal  
*Chondrus crispus* Lyngb. very broad  
*Chondrus crispus* Lyngb. narrow  
*C. norvegicus* Lamour.  
*Rhodymenia palmata* Grev. var. *soboliferus*  
*R. jubata* Grev.  
*R. laciniata* Grev.  
*Chylocladia kaliformis* Hook.  
*C. articulata* Grev.  
*C. ovalis* Hook.

*Plocamium coccineum* Lyngb.  
*Nitophyllum punctatum* Grev.  
*N. hilliae* Grev.  
*Delessaria alata* Lamour.  
*Delessaria alata* var. *angustissima*  
*Laurencia pinnatifida* Lamour.  
*Laurencia pinnatifida* var. *osmunda*  
*L. dasyphylla* Grev.  
*L. tenuissima* Grev.  
*L. caespitosa* Lamour.

*Polysiphonia elongata* Grev.  
*P. fastigiata* Grev.  
*Dasya coccinea* Ag.  
*Callithamnion virgulatum* Harv.  
*Ptilota sericea* Gmel. (sp.)  
*Furcellaria fastigiata* Lamour.  
*Polyides rotundus* Grev.  
*Melobesia pustulata* Lamour.  
*Corallina officinalis* Lamour.  
*Janira rubens* Lamour.

*Tranabo Cove and Tragemona.* Both of these bays provide excellent dredging grounds, which are composed of firm sand or fine gravel. On account of its larger size and the sandier nature of the main area of its bottom *Tragemona* yields a larger number of both species and individuals. With the exception of the strands the boundaries of both consists of much indented rock.

Through the strand of *Tragemona* (Plate XXV, Phot. 13) runs the effluent from the fresh-water Lough alluded to in an earlier part of this paper, and fringed by a marsh, which widens out to the north, and from which the area probably derives its name—*Traigh na Mona*, the Strand of the Marsh or Bog.

On the west *Tragemona* leads into a smaller cove, *Tralispean* (Plate XXV, Phot. 12), whose strand is now slaty gravel, but which was once probably of sand, for the name means "the Smooth Strand," and above high water mark there is a small sandbank, held together by grasses, *Lotus corniculatus* var. *crassifolius* Pers. and small plants of *Anthyllis vulneraria* among which are scattered plants of *Eryngium maritimum* L. Into the strand flows a small stream, the *Bealariree*, whose upper region often floods the narrow flat valley through which it flows, and from this a large area westwards and northwards of the strand, while to the north-west it connects with a large expanse covered with common reed, *Phragmites vulgaris* Druce, which used to be cultivated for thatching and other purposes. Eastwards this joins a marshy area, on part of which a fen carr, with *Myrica gale* L. sweet gale, *Salix repens* L. dwarf willow, *Alnus rotundifolia* Mill, etc. is developing. The whole of this region is extremely interesting on account of the transitions it shows from coarse heather-gorse moor, and maritime associations, to moor water, reed marsh, bog, fen, and fen carr, back to moorland.

The following list of animals obtained by dredging in *Tragemona* includes many characteristic arenicolous species (marked "a"), in addition to numerous offshore forms, and provides an interesting contrast with the main fauna of Barloge Channel. Many species of algae, especially of small Florideae, which have been torn from their substratum by the waves, are taken in the dredge, but have not been identified.

## DREDGING TRAGEMONA BAY.

## COELENTERATA

## HYDROMEDUSAE

## GYMNOBLASTEAE

Hydractinia echinata Fleming

## CALYPTOBLASTEAE

Obelia geniculata (L.)  
 Antennularia antennina (L.)  
 Plumularia setacea (Ellis)  
 Sertularia polyzonias (L.)

## ANTHOZOA

## ZOANTHARIA

Metridium senile (Linn.)

## ECHINODERMATA

## ASTEROIDEA

Luidia sarsi (D. and K.) a  
 Astropecten irregularis (Penn.) a  
 Asterias glacialis L.  
 A. rubens L.

## OPHIUROIDEA

Amphiura elegans (Leach)  
 Ophiura ciliaris (L.) a  
 O. albida Forbes  
 Ophiothrix fragilis (Abild.)

## ECHINOIDEA

Echinus esculentus L.  
 Echinus miliaris Gmel.  
 Echinocardium cordatum (Penn.) a

## HOLOTHUROIDEA

Cucumaria saxicola Brady and Robertson\*

## NEMERTINEA

Lineus longissimus (Gunn)

## ANNELIDA

Nephtys caeca (Müller) a  
 Pomatoceros triqueter (L.)  
 etc.

## POLYZOA

Scrupocellaria reptans L.  
 Membranipora membranacea L.  
 etc.

## CRUSTACEA

## ENTOMOSTRACA

Chondracanthus lophii Johnst.  
 Balanus porcatus da Costa

## ARTHROSTRACA

Idotea baltica (Pallas)  
 I. linearis (Penn.)  
 I. emarginata (Fabricius)  
 Amphipoda numerous

## DECAPODA

Cancer pagurus L.  
 Pilumnus hirtellus (L.)  
 Carcinus maenas (Penn.)  
 Maia squinado (Herbst.)  
 Hyas araneus (L.) a  
 Pisa tetraodon (Penn.)  
 Inachus dorsettensis (Penn.)  
 Stenorhynchus rostratus L.

Portunus puber (L.)

P. depurator (L.)

P. marmoreus Leach

P. corrugatus (Penn.)

P. arcuatus Leach

Corystes cassivelaunus Penn. a

Porcellana longicornis (L.)

Galathea squamifera Leach

Eupagurus bernhardus L.

E. prideauxii (Leach)

Hippolyte varians Leach

Leander serratus (Penn.)

Crangon vulgaris L. a

## PYCNOGONIDA

Nymphon rubrum Hodge

## MOLLUSCA

## PELECYPODA

Nucula nitida G.B.S.  
 Lucinopsis undata (Penn.)  
 Dosinia lupulina  
 Venus verrucosa L.  
 Cardium tuberculatum  
 Lutraria elliptica Lmk. a  
 Ensis ensis (L.) a  
 Kellia minuta  
 K. suborbicularis (Mont.)

## GASTROPODA

Helcion pellucidum (L.)  
 Gibbula umbilicata (Mont.)  
 G. cineraria (L.)  
 Calliostoma zizyphinus (L.)  
 Phasianella pullus L.  
 Rissoa spp.  
 Trivia europaea (Mont.)  
 Buccinum undatum (L.) shell

## TECTIBRANCHIATA

Aplysia punctata Cuv.  
 Philine aperta (L.)  
 Acera bullata Müller

## NUDIBRANCHIATA

Doris flammea A. and H.

## CEPHALOPODA

Sepia officinalis L. spawn

## PISCES

Scyllium canicula (L.)  
 Raia batis L. a  
 R. clavata (L.) a  
 R. maculata Mont. a  
 Nerophis lumbriciformis (Yarrell)  
 Pleuronectes platessa (L.) a  
 P. limanda (L.) a  
 P. microcephalus Donov. a  
 Rhombus laevis Rondel. a  
 Arnoglossus megastoma Day a  
 Solea vulgaris Quesn. a  
 S. lutea (Risso.) a  
 Gobius ruthensparri Euphras.  
 Cottus scorpius (L.)  
 Callionymus lyra L.  
 Zeus faber L.  
 Centronotus gunnellus (L.)

## FAUNA, GENERAL.

No really systematic collecting of the general terrestrial fauna has been attempted yet, but a good many data have been accumulated. These show that the mammals of the district include *Erinaceus europaeus* L. the common hedgehog (usually called porcupine locally), *Sorex minutus* Lin. the lesser or pigmy shrew, *Canis vulpes* L. the fox, *Mustela vulgaris* Erxl. the weasel, *Meles taxus* L. the badger, *Lutra vulgaris* Erxl. the otter, *Oryctolagus cuniculus* (L.) the rabbit, and of course, *Mus musculus* L. and *M. decumanus* Pall. the house mouse and brown rat. Probably the pine marten *Mustela martes* L. occurs too, but we have met with only verbal evidence that such is the case. (*Phoca vitulina* L. the common seal, is abundant throughout the year, and small shoals of porpoise, *Phocaena communis* Lesson, appear at times.) Of the seventy species of birds noticed the most prominent on account of their numbers, are the common curlew (*Numenius arquata* (L.)), the wren (*Troglodytes parvulus* K. L. Koch) and the stonechat (*Pratincola rubicola* (L.)); while the scarcest include the hoopoe (*Upopa epops* L.), the kingfisher (*Alcedo ispida* L.) and the chough (*Pyrrhocorax graculus* (L.)).

*Lacerta vivipara* Jacquin, the common lizard, which is abundant, especially around Lough Ine, is the only reptile found (with the exception of the turtle previously mentioned, as having been washed ashore). *Molge vulgaris* L. the common newt, locally believed to be a lizard, is very abundant, more particularly about Baltimore, and often hibernates beneath large stones on the shore of the estuary of the Ilan and sometimes even on the seashore, which must be washed by spring tides. *Rana temporaria* L. is met with only occasionally, though its spawn is sometimes abundant.

Insecta and Arachnida are plentiful, some of them unpleasantly so, in particular *Haematopota pluvialis* L. the clegg, known in many parts as the "horse doctor," and *Ixodes ricinus* L. the sheep and cattle tick. *Argyroneta aquatica* Latr. the water spider and *Epeira diademata* (Clk.) the large cross-spider are the most noticeable of the Araneida, on account of the numbers in which they occur. On account of their brilliant coloration *Cicindela campestris* L. the tiger beetle and *Cetonia aurata* L. the rose chafer are two of the most obvious members of the Coleoptera. Of the Lepidoptera, the Rhopalocera are well represented, five species of Vanessa, including *V. polychloros* L. the large tortoiseshell, *V. cardui* L. the painted lady, *Euchloe cardamines* L. the orange tip, and *Argynnis aglaia* L. the dark green fritillary, being especially prominent. *Smerinthus ocellatus* the eyed hawk-moth, *Lasiocampa quercus* L. the oak eggar, and *Saturnia pavonina* L. the emperor, are some of the outstanding Heterocera. Though members of the Odonata, Hymenoptera, and other orders abound but few of them have been identified yet, and the same is true of the Myriapoda, Isopoda, Crustacea and Mollusca.

Reference has been made already to the occurrence of *Orthezia* sp. and *Salda pallipes* F. in the Goleen.

Species identified to date number 580 plants and 820 animals. These numbers will probably be at least trebled if the work continues as it has started, for, as pointed out at the beginning of this report, our results are incomplete in every direction, while some groups have not been dealt with at all. It is hoped, however, that sufficient has been said to attract serious workers to the area under consideration.

One other inducement may be proffered. This is the accessibility of the famous regions of south-west Ireland, well known for the interest of their natural history and for their beauty, such as Killarney and the Macgillicuddy Reeks.

Acknowledgments are due to those who have made the work possible, and to others who have helped with identifications, and in many other ways. The main debt is due to Dr Lloyd Praeger and to Mr Richard Southern, as is shown in the introduction, and to the late Miss Elizabeth Crawford Hayes, whose generosity is doing so much for biology in the National University of Ireland. Grants for apparatus from the Royal Dublin Society and the Government Grants Committee of the Royal Society have made the hydrographical work, dredging and tow-netting possible. Considerable help has been given by Mr A. W. Stelfox of the National Museum, Dublin, and by many members of the staff of the British Museum, Natural History, in particular by Capt. A. K. Totton and Mr M. Burton. Finally, Mr Southern's MSS. list of species, a copy of which he most kindly let me have, has been of the greatest assistance.

To all these, and to the authorities of University College, Cork, for allowing part of the Crawford Bequest to be used on this work, deepest thanks are tendered, and especially to Mr Michael Donovan, the farmer at Barloge, without whose interest the chief work could not have been undertaken.

## PRELIMINARY OBSERVATIONS ON THE PHAEOPHYCEAE OF LOUGH HYNE (INE)

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THROUGH the kindness and hospitality of Prof. Renouf<sup>1</sup>, I was able to visit the Lough Hyne district during July, 1930, and to carry out a number of observations relating both to the epiphytism and to the method of over-wintering of certain species of the Phaeophyceae. Favoured with a continued period of fine weather, it was possible to carry out preliminary work on the general ecology of marine algae in the area. The present preliminary paper is presented in the hope that other algologists will visit the district, which is exceptionally rich not only in the number of species, societies and associations of marine algae, but also in ecological problems which arise because of the peculiar situation of the lough at the top of Barloge Creek (affecting the length of exposure of its littoral species) and because of the almost sudden transition from exposed to sheltered conditions. A series of future visits have been planned and it is hoped to deal fully in a later paper with the algal communities which, though following in the main the characteristics enumerated by Cotton (*Clare Island Survey*, Part 15, 1912), present variations and exceptions, instances of which will be given in the second part of this paper dealing with the distribution of the Fucaceae in the lough.

### PART I. SYSTEMATIC LIST WITH ECOLOGICAL NOTES.

This list, which follows the classification adopted by Batters (*Journ. Bot.* 1902), is of course not exhaustive, including only those species found during early July, but it will indicate very clearly the wealth of species to be found in so restricted an area. The following abbreviations are used: BC = Barloge Creek; SB = Southern's Bay; R = Rapids; LH = Lough Hyne; CI = Castle Islands; N., S., E., W., for North, South, East, West.

*Desmarestia viridis* Lamour. BC, rather rare, in quiet water associated with *Zostera*, *Dictyosiphon foeniculaceus*, *Asperococcus fistulosus* and *A. bullosus*.

*D. aculeata* Lamour. BC, more frequent on western than eastern side. Bullock Island. Summer condition beginning July 1st, some hairs bearing epiphytic Diatoms.

*D. ligulata* Lamour. Occasional on W. mainland of BC, especially opposite Bullock Island. Fruiting and bearing several epiphytic *Ectocarpus* spp. The relative vertical distribution of *D. aculeata* and *D. ligulata* in the Laminaria association of moderately sheltered coasts would repay attention as the former is subarctic and the latter warm-boreal. In BC, *D. ligulata* would appear to be confined to the Alaria sub-association of the Laminarietum.

*Dictyosiphon foeniculaceus* Grev. Frequent but local in LH. Especially noticeable on the N. side of CI. Also epiphytic on *Cystoseira ericoides* along south shore of LH.

<sup>1</sup> See the paper by Prof. Renouf on p. 410 which includes maps of the area.



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*D. hippuroides* Kütz. Quiet waters in BC, and LH(S.).

*Phaeostroma pustulatum* Kck. On *Laminaria saccharina* in SB, and on *L. saccharina* f. *Phyllitis* in LH(E.).

*Litosiphon pusillus* Harv. A frequent epiphyte on *Chorda filum*, *Laminaria saccharina* and occasionally on *Saccorhiza polyschides*. On *Zostera marina* in BC, but not on *Zostera* in LH.

*L. Laminariae* Harv. Abundant on the stipe and upper part of lamina of *Saccorhiza polyschides* in R, and frequent on *Alaria esculenta* at the mouth of BC.

*Stictyosiphon subarticulatus* Hauck. A few plants were found near CL, and in BC at the edge of the Chorda beds.

*Punctaria plantaginea* Grev. In SB, and rare plants in LH(S.).

*P. latifolia* Grev. Not uncommon in quiet waters and sheltered situations as an epiphyte on *Asperococcus fistulosus*, *Cystoseira ericoides*, *C. granulata*, *Himanthalia lorea*, *Scytosiphon lomentarius* and *Saccorhiza polyschides*. It bears in such sheltered habitats a varied epiphytic flora of its own including *Leathesia difformis*, *Asperococcus fistulosus*, *Sphacelaria cirrhosa*, *Ceramium rubrum*, *Callithamnion* sp.

*P. tenuissima* Grev. On *Zostera marina* in Chorda beds, and on *Cystoseira ericoides* in BC.

*Desmotrichium undulatum* Rke. On *Zostera marina*.

*Phyllitis Fascia* Kütz. Infrequent and local along LH(S.), and SB. Epiphytic on *Fucus vesiculosus* and *Scytosiphon lomentarius* as well as free-growing.

*Scytosiphon lomentarius* J. Ag. Distributed throughout the area, but not common. Good growths in Trenabo Bay and in rock pools on Bullock Island, and in SB. Especially prominent in some high tide pools associated with *Enteromorpha intestinalis*. Epiphytic on *Asperococcus fistulosus* in quiet bays, and on *Zostera marina* in BC.

*Asperococcus fistulosus* Hooker. A very common member of the vegetation of sheltered bays, growing freely on such algae as *Himanthalia lorea*, *Fucus vesiculosus*, *Cystoseira ericoides*, *C. granulata*, *Laminaria saccharina*, *Punctaria latifolia* and *Cladophora* sp. as well as on a rocky or sandy substratum. It is particularly abundant in SB and LH(S.), and bears a rich epiphytic flora consisting of *Myriotrichia filiformis*, *M. claviformis*, *Sphacelaria cirrhosa*, *Ceramium rubrum*, *C. strictum*, filamentous Diatoms and *Ectocarpus* sp.

*A. fistulosus* f. *vermicularis* Griff. Found as an epiphyte on *Cystoseira ericoides* in LH.

*A. bulbosus* Lamour. Locally abundant in quiet waters especially SB, often reaching 2-3 feet in length and associated with *A. fistulosus* as an epiphyte on the larger Fuci. In LH, it is confined to the S. shore and to the *Cystoseira* zone.

*A. compressus* Griff. Hitherto apparently unrecorded for Ireland, four specimens of this alga were found when sorting material collected for studies in epiphytism. Locality SB. The basal holdfast was associated with *Urospora*, *Enteromorpha*, *Bangia* and *Ectocarpus* sp. and it would appear to have been growing in the *Bangia-Urospora* association, rather above the usual level for the *Asperococci*.

*Streblonemaceae*. No critical study of this family was made.

*Ectocarpus* Lyngb. Owing to the difficulty of identifying many species under field conditions, and to the fact that attention was mainly directed to general ecological problems, no systematic study of this genus was made. The following were found in the course of general observations:

*E. Stilophorae* Crn. On *Stilophora rhizoides* LH(E.).

*E. tomentosoides* Farlow. On *Himanthalia lorea*.

*E. velutinus* Kütz. On *Himanthalia lorea*, fairly frequent.

*E. confervoides* Le Jol. Abundant.

*E. siliculosus* Kütz. Frequent, often epiphytic on Fuci and *Himanthalia lorea*.

*E. fasciculatus* Harv. A very common epiphyte on *Saccorhiza polyschides*, *Laminaria digitata*, *Alaria esculenta* and less common on *Himanthalia lorea*.

*E. tomentosus* Lyngb. Old plants were found occasionally attached to Fuci in LH.

*E. Hincksii* Harv. Frequently encountered as an epiphyte on *Saccorhiza polyschides*, *Laminaria Cloustoni*, more rarely on *L. digitata*.

*E. granulatus* Ag. In deep waters in both exposed and sheltered habitats, free-growing or epiphytic on *Rhodomenia palmata* and *Laminarias*. Not uncommon in R.

- Pylaiella littoralis* Kjellm. Abundant everywhere, even where fresh water enters the Lough. Common in BC as an epiphyte on *Chorda*, *Zostera*, *Ascophyllum nodosum*.
- Myriotrichia claviformis* Harv. A common epiphyte on *Asperococci*, *Zostera marina*, *Chorda filum* and *Scytosiphon lomentarius*.
- M. filiformis* Harv. More abundant than the previous sp. and found in addition on *Mesogloia vermiculata* and *Corallina officinalis*.
- Myriactis pulvinata* Kütz. On tips of branches and receptacles of *Cystoseira ericoides* and *C. granulata* in BC, especially when growing in pools near h.w.m.
- M. Haydeni* Batt. Occasionally found on *Scytosiphon lomentarius*.
- M. stellulata* Batt. Rare on *Dictyota dichotoma*.
- Elachistea fucicola* Fries. On decaying receptacles of Fuci, in R, BC, and LH(S.).
- E. flaccida* Aresch. Common as an epiphyte on *Cystoseira ericoides* and *C. granulata* in BC. On *C. granulata* in LH(S.). On *Himanthalia lorea* in SB. Particularly in deep high-tide pools where there is little renewal of sea water, except at spring tides.
- E. scutulata* Duby. Frequent on *Himanthalia lorea*.
- Giraudia sphacelarioides* Derb. et Sol. Plants bearing tufts of basal sporangia and older plants with pustulate sori were found on *Cystoseira* near SB and *Zostera* in BC.
- Sphacelaria radicans* Harv. Occasional on rocks with sandy mud covering.
- S. cirrhosa* Ag. No attention was paid to the various forms under which this very variable alga occurs. It is abundant as an epiphyte on a number of algae (18 different host species were recorded) and frequently free growing. Propagulae were being produced freely and were found germinating on *Dictyota* and *Punctaria*.
- Cladostephus spongiosus* Ag. Occasional in LH and BC. It shows a preference for sandy rocks.
- C. verticillatus* Ag. Rare, found only in deep shaded channels and near cave mouths.
- Myrionemaceae*. A large number of algae bore members of this family as epiphytes. They await accurate identification and will be treated in a future paper. *Myrionema strangulans* Grev. and *Ascoecyclus orbicularis* Magn. were abundant.
- Ralfsia clavata* Farlow. On bare rock surfaces associated with *Verrucaria* sp.
- R. verrucosa* Aresch. Abundant in LH in regions where only the common Fuci are found, often reaching considerable depth as a constituent of the encrusting algae association of pebbles and stones.
- Stilophora rhizoides* J. Ag. Abundant in LH(S. and E.) and S. of CI.
- Spermatocnusus paradoxus* Kütz. Not uncommon in LH(S.) and S. of CI, but especially noteworthy along the E. shore where there is a good flow of water. In deeper water than the preceding.
- Chordaria flagelliformis* Ag. Rather rare, in pools and deep water on W. side of BC, especially where overhanging rocks cast deep shade.
- Mesogloia vermiculata* Le Jol. Frequent, noticeably in SB and LH(S.).
- M. Griffithsiana* Grev. In Trenabo Cove and on Bullock Island. Rare.
- Castagnea virescens* Thur. Rock pools in Trenabo Cove; on Bullock Island. Also near R, and occasionally along LH(S.).
- C. Zosteræ* Thur. Frequent on *Zostera marina* in BC.
- Petrospongium Berkeleyi* Näg. Frequent in *Ralfsia* zone in BC, but rare in LH.
- Leathesia difformis* Aresch. Abundant but local. Epiphytic on *Asperococcus fistulosus*, *Cystoseira ericoides*, *C. granulata*, *Himanthalia lorea*, *Corallina* sp., *Mesogloia vermiculata* and *Punctaria latifolia*. Especially prominent on gently shelving rocks.
- Chorda filum* Stackh. Forming "fields" in the centre of the upper part of BC and in isolated patches in LH (see Table I). Abundantly clothed with epiphytes which show a definite zoning; *Sphacelaria cirrhosa* near the base; *Myriotrichia filiformis* and *Litosiphon pusillus* midway and almost pure *L. pusillus* towards the apex.
- Laminaria saccharina* Lamour. Common both in BC, and on S. and lower E. shores of LH. The forms *latissima* Turn. and *Phyllitis* Le Jol. are also present. In Lough Hyne it is always densely clothed with epiphytes.

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*L. digitata* Lamour. Plentiful in BC, but not spreading beyond the entrance to the Rapids in LH.

*L. Cloustoni* Edm. Common in deep water at entrance to BC, especially near Bullock Island. Higher up the creek it is broken and discontinuous in distribution.

*Saccorhiza polyschides* Batt. Locally abundant, noticeably in R, and near mouth of BC. In R, plants of large dimensions occur, 7-8 feet in length. Epiphytes show definite zoning, of which the following is an example:

On bulbous base: *Ceramium rubrum*, *Sertularia operculata*, *Scrupocellaria* sp., *Hecatonema* sp., *Schizoporella hyalina*, *Spirorbis* sp., *Hymeniacion sanguineum*, *Balanus balanoides*.

On furbelows: *Obelia geniculata* and *Schizoporella hyalina*.

On stipe: *Litosiphon Laminariae*, *Ectocarpus Hincksiae*, *Obelia geniculata*, *Ceramium rubrum*, *Enteromorpha* sp., *Polysiphonia* sp., *Punctaria latifolia*, and sporeling *Fucus serratus*.

On lamina: lower 4 ins. continues *Ectocarpus Hincksiae* of stipe; gradually *E. Hincksiae* thins out and *Litosiphon Laminariae* becomes abundant, covering the last 2-2½ feet of the lamina.

*Alaria esculenta* Grev. Abundant at mouth of BC, especially on the more precipitous rocks. *Litosiphon Laminariae* and *Ectocarpus fasciculatus* occur as epiphytes.

*Cutleria multifida* Grev. Found on a visit to a bay E. of Baltimore.

*Fucus ceranoides* L. In five places in Lough Hyne (see Table I) in brackish water.

*Fucus spiralis* L. and var. *platycarpus* Batt. Abundant (see Table I).

*F. vesiculosus* L. Abundant in BC, and LH (see Table I).

*F. serratus* L. Abundant in BC, and R, but local in LH (see Table I).

*Ascophyllum nodosum* Le Jol. Abundant but disappearing near mouth of BC.

*Pelvetia canaliculata* Dene. et Thur. Abundant (see Table I).

*Himanthalia lorea* Lyngb. Plentiful in BC, but in patches only in LH (see Table I). In LH it is frequently covered with epiphytes of which the following are typical:

On vegetative portion: *Sphacelaria cirrhosa*, *Gelidium corneum*, *Microcladia glandulosa*, *Melobesia* sp.

On receptacles: *Punctaria latifolia*, *Dictyota dichotoma*, *Sphacelaria cirrhosa*, *Ectocarpus fasciculatus*, *E. siliculosus*, *Asperococcus fistulosus*, *Leathesia difformis*, *Elachistea scutulata*, *E. velutinus*, *Enteromorpha* sp., *Cladophora* sp., *Laminaria saccharina* f. *Phyllitis* and *Rhodochorton* sp.

*Halidrys siliquosa* Lyngb. Rare, found only in a few pools in Trenabo Cove and on W. of BC.

*Cystoseira ericoides* Ag. Abundant in LH(S.); scattered and locally abundant in BC.

*C. granulata* Ag. Associated with the previous sp. in LH, but rare, except in pools, in BC. Typical epiphytes:

On *C. ericoides*

*Leathesia difformis*, *Elachistea stellaris*  
*Sphacelaria cirrhosa*, *Melobesia* sp.  
*Corallina officinalis*, *Ceramium* spp.  
*Chytocladia ovalis*, *Cladophora* sp.  
*Chaetomorpha tortuosa*, *Punctaria latifolia*, *Asperococcus fistulosus*  
*Callithamnion* sp., *Gelidium* sp.  
*Elachistea flaccida*, *Myriactis pulvinata*

On *C. granulata*

*Ceramium rubrum*, *Melobesia* sp.  
*Asperococcus fistulosus*,  
*Punctaria latifolia*, *Stilophora rhizoidea*, *Elachistea flaccida*,  
*Spermatococcus paradoxus*,  
*Sphacelaria cirrhosa*,  
*Myriactis pulvinata*.

*Dictyota dichotoma* Lamour. In rock pools in BC. Occasional in LH, especially near the Goleen.

f. *intricata* Ag. In deep rock pools and deep water near cave in BC. Usually free growing but sometimes epiphytic on *Corallina rubens*.

## PART II. THE DISTRIBUTION OF THE FUCACEAE IN LOUGH HYNE.

*Fucus ceranoides*, *F. spiralis*, *F. vesiculosus*, *F. serratus*, *Ascophyllum nodosum*, *Pelvetia canaliculata*, *Himanthalia lorea*, *Cystoseira ericoides* and *C. granulata* occur with varying frequency in Lough Hyne, and the general extent of their distribution may be seen by reference to Table I. It will be noticed that the *Cystoseiras* are confined to the S. shore, the lower part of the E. shore, with a few scattered plants to the S. of the Castle Islands, a distribution characteristic also of *F. serratus* which, however, does not extend quite so far along either the S. or E. shores and is less prominent on Castle Islands. It is evident that these three algae require a constantly changing medium, for they are found in those parts of the lough where the current sweeps steadily as it enters from the Rapids and as it pours out at ebb tide. In the Rapids themselves *F. serratus* is plentifully found on both sides, but for the two *Cystoseiras* the conditions here are too turbulent, and they begin to appear in the lough just at the point where the swirling and eddying waters are transformed into a steady but swiftly flowing current: along with *F. serratus*, they again disappear as the current weakens against the resistance of the lough waters. The incoming tide, deflected in part by the bend 26-29 on the E. shore and travelling naturally towards the wider opening between the W. of Castle Islands and the W. mainland, creates a constantly changing medium along the S. shore of the island and around the headland 3-6; and here again the three algae appear, though less prominently than on the mainland. Through the narrow channel opposite 26, water rushes too rapidly for the *Cystoseiras*, but *F. serratus* has quite a luxuriant growth (Islands 14-16), confirming the view that whilst a rapidly changing medium is required by all three, anything approaching a turbulent condition prevents the growth of the *Cystoseiras*.

The distribution of *F. ceranoides* is well marked and distinctive, being confined to five areas where fresh water enters the lough. At all places except 15 it is merely trickling drainage water and the alga is poorly developed, but at 15, where a stream enters, the growth is extensive and the plants of normal size.

The presence of *Himanthalia lorea* in the lough is puzzling, for on the coast of Wales it is confined to exposed positions with considerable surf action, a habitat characteristic of the plant in Co. Mayo (Cotton, *Clare Island Survey*) and on the Faerøes coasts (Börgesen, *Botany of the Faerøes*, p. 733). Yet occasional plants were found in the Goleen which is probably the most sheltered part of the lough; well up on the W. shore 6-9; along the S. shore; and scattered plants occur on the shores of Castle Islands. It is interesting to note that its distribution in the lough is very similar to that of *Laminaria saccharina*, a plant that normally requires rather quieter conditions and a weaker current than other Laminarias. The spores of many exposed species

Table I. Phaeophyceae of Lough Hyne.

	White blazes appearing on map	West shore	North shore	East shore
<i>Pelvetia canaliculata</i>	1-2 2-3 3-4 4-5 5-6 6-7 7-8 8-9 9-10 10-11 11-12 12-13 13-14 14-15 15-16 16-17 17-18 18-19 19-20 20-21 21-22 22-23 23-24 24-25 25-26 26-27 27-28 28-29 29-30 30-31	+	+	+
<i>Fucus spiralis</i>	+	+	+	+
<i>Ascophyllum nodosum</i>	+	+	+	+
<i>Fucus vesiculosus</i>	+	+	+	+
<i>Fucus serratus</i>	+	+	+	+
<i>Fucus ceranoides</i>	+	+	+	+
<i>Himantalia lorea</i>	+	+	+	+
<i>Cystoseira ericoides</i>	+	+	+	+
<i>Cystoseira granulata</i>	+	+	+	+
<i>Laminaria digitata</i>	+	+	+	+
<i>Laminaria saccharina</i>	+	+	+	+
<i>Saccorhiza polyschides</i>	+	+	+	+
<i>Alaria esculenta</i>	+	+	+	+
<i>Chorda filum</i>	+	+	+	+
<i>Stilophora rhizoides</i>	+	+	+	+
<i>Dichyosiphon foeniculaceus</i>	+	+	+	+
<i>Zostera marina</i>	+	+	+	+





of marine algae must be carried into the lough with the sweep of the tide through Barloge Creek and the Rapids, yet apart from *Himanthalia* they fail to establish themselves there. The usually recognised factors which determine horizontal (as distinct from the vertical) distribution—such as salinity, tides and currents, nature of coast and of substratum—are not in themselves sufficient to account for the appearance in the lough of *Himanthalia* alone of the exposed species whose spores may be carried there. As yet, the intimate relationships which exist under marine conditions between plants and animals have not been carefully studied. The influence of biotic factors, long recognised as of great importance in the ecology of land plants, has hardly been touched upon in algological literature. It is evident that many of the smaller marine animals devour, amongst other food material, the spores of marine algae, and just as a selective capacity is seen in the case of antherozoids in relation to oospheres, and in the case of nematode parasites in relation to receptacles of the Fuci, so a similar selective capacity may be found to prevail between certain marine animals and the spores and germings of marine algae. Discontinuous horizontal distribution, though often accounted for in terms of anchorage demand, may depend also on the depredations of marine animals, and to this problem, illustrated by the case of *Himanthalia*, it is hoped to return on the occasion of a future visit to Lough Hyne. It is of course possible that the large and comparatively heavy oospores of *Himanthalia* are able to come to rest, and in the absence of serious competition may begin to germinate, whilst lighter spores, e.g. those of *Alaria*, *Laminaria digitata* and *L. Cloustoni* are swept out of the lough with the ebbing tide.

The four remaining Fucaceae are, except in a few areas, generally distributed along the whole of the shore of the lough. A study of their relative vertical and horizontal distribution reveals the importance of three ecological factors:

(1) *The rise and fall of the tide.* Except near the Rapids the rise and fall is about 4 ft. in Lough Hyne as compared with about 12 ft. in Barloge Creek (for spring tides). This restricted rise and fall affects the vertical depth or zoning of the Fuci rather strikingly as the following table shows:

Table II.

	Vertical depth of			
	<i>Pelvetia canaliculata</i>	<i>Fucus spiralis</i>	<i>Ascophyllum nodosum</i>	<i>Fucus vesiculosus</i>
Barloge	1 ft.—1 ft. 3 in.	10 in.—1 ft. 6 in.	3–5 ft.	4–7 ft.
Lough Hyne	9 in.	6 in.	1 ft. 6 in.—2 ft.	2–3 ft.

Experiments by Baker (*New Phyt.* 8, 196; 9, 54) have shown the effect of varying periods of submergence and exposure on the growth of the Fuci. Observations in Lough Hyne show that *Pelvetia* can withstand, without obvious detriment to growth, an increase above the normal period of submergence: that *F. spiralis* is much more sensitive and its vertical range is therefore

very restricted: that *F. vesiculosus*, with a vertical range of 2-3 ft. below the zone of *F. spiralis*, can live under conditions of complete submergence and yet retain a healthy, though rather bushy, appearance.

(2) *Nature of substratum*. Along many parts of the shore the upper region, near or just below high water mark, consists of small rounded pebbles or sharp-edged stones. Under such conditions anchorage is precarious, for winds create considerable wave action along the shore, and only scattered and dwarf plants of *Pelvetia* are found. When the whole shore down to low water mark is similarly constituted, the area is devoid of Fuci, or only a few dwarf plants appear. Below low water mark however, *F. vesiculosus* (and occasionally *Laminaria saccharina*) is often found, especially if the slope is very gradual. Winds, and hence wave action, most often accompany a rising tide, so that at low water conditions are in general more quiet, and anchorage is obtained. Occasionally in such regions the stones are cemented by mud, thus forming a solid substratum, and *F. vesiculosus* is abundant. It frequently happens that on such stony shores boulders and even rocks project. *Ascophyllum* and *F. vesiculosus* then occur plentifully, and a series of comparative observations on the number and condition of plants growing on stony areas with occasional boulders and rocks shows the importance of suitable anchorage in determining horizontal distribution. Of the four Fuci here considered, *Ascophyllum* requires the firmest anchorage, and with decreasing size of stones, first *F. spiralis*, then *F. vesiculosus* and finally *Pelvetia* disappear. The ascendancy which *Ascophyllum* gains on large boulders is strikingly shown in area 34-35, where both boulders and stones occur in the *Ascophyllum-F. vesiculosus* zone. The former is confined wholly to the boulders and the latter to the stones.

(3) *Angle of slope*. Though well recognised as an important factor determining the distribution of numerous algal communities, the effect of the angle of slope on the relative distribution of the common Fucaceae in sheltered regions has not received much attention. The following summary of observations in Lough Hyne will bring out its importance in this respect.

(a) Nowhere in the lough is there a flat rocky shore with wide zones of the Fucaceae; where the shore is fairly gently sloping it is usually stony and anchorage is poor, the plants being poorly developed and scattered. The greater part of the shore is rocky and steep, and with increasing steepness of the angle of slope there is a corresponding narrowing of the width of the zone of each species, though its bathymetric range remains much the same.

(b) Where rocks or walls descend sheer into the water and their surface is almost smooth, either no Fuci are found, e.g. 15-18, or zones of *Pelvetia* and *F. spiralis* only occur, e.g. 29-30, 22-23. With a roughening and pitting of the surface *Ascophyllum* and *F. vesiculosus* are found, the former being usually much more prominent as it appears to be able to grow much more vigorously in a hanging position, whilst *F. vesiculosus* (like *F. serratus*) prefers a horizontal or gently sloping substratum. This contrast is well seen on the

rocky promontory and the island near the quay 17-18. In certain regions, e.g. near 11, where a steep rock arises from a shelving shore *Ascophyllum* is at first the sole occupant, but as a general rule on sheer rocks, with a roughened surface, all four species occur, with the *Ascophyllum* belt best developed. There are, however, some exceptions, e.g. 4-6 where *Ascophyllum* disappears on steep rocks and *F. vesiculosus* remains.

(c) Where rocks are overhanging and the surface concave, as e.g. on the E. side of the entrance to the Goleen, and at a few points along the E. shore near the Rapids, no Fuci are able to find attachment. If small ridges or shelves project, dwarf plants appear, the species depending on the vertical height above low-water mark. In one of the inlets in lower Barloge Creek the S. entrance is concave and quite devoid of Fuci, whilst the N. entrance, though rather steeply inclined, bears a good growth of all five.

For purposes of comparison with other areas, the Fucaceae whose general distribution is described above may be divided into two associations; a littoral Fucaceae Association and a sub-littoral *Cystoseira* association. The floristic differences between the Irish and Continental Fucaceae associations have been dealt with by Cotton (*loc. cit.* p. 26) and need not be treated here. The Fucaceae association of Lough Hyne is in the main similar to that of sheltered bays in Co. Mayo as described by Cotton, but with the total vertical range and that of the constituent species much telescoped owing to the small rise and fall of the tide. There is a notable difference, however, in the restricted distribution of *F. serratus* in Lough Hyne. This alga clearly requires a rapidly changing medium for its normal growth, and, as has been shown, it is confined to those parts of the lough where the current flows swiftly along. Discontinuity in the distribution of the other species is due to the nature of the substratum (affecting anchorage) and the angle of slope. The sub-littoral *Cystoseira* association may be considered as a continuation of the Laminarietum of sheltered bays, and floristically it is not dissimilar to the Pebble-attached association of quiet bays (Cotton, *loc. cit.* p. 73) though complicated by the presence of *Himanthalia lorea*, whose appearance in the lough probably depends on biotic factors as yet little understood. Fuller treatment of this association will appear in a later paper dealing with the algal communities of Lough Hyne and district.

# STUDIES IN THE ECOLOGY OF WICKEN FEN

## I. THE GROUND WATER LEVEL OF THE FEN

By H. GODWIN.

(With Plate XXVII and 20 Figures in the Text.)

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### INTRODUCTION.

THE ecological studies described in this and the following papers have to do with the successional and distributional relations of the plant communities of Wicken Fen, near Cambridge, England, a general account of which has already been given by myself and Prof. Tansley (1). In the present series of studies problems are raised of the nature of control of the distribution of communities by environmental factors, especially by the water level. The first paper deals with the investigation of the fen water levels, and the manner in which they are controlled by many factors, including that of water consumption by the vegetation itself. The second paper<sup>1</sup> which will appear in the next issue of this *Journal* will begin with a consideration of the height of the peat surface in the fen and the configuration and movements of the water table below it, and proceed to a detailed consideration of the nature of the control exercised by the water-level/ground-level relationships upon the distribution of plant communities in the fen.

Consideration of the ecology of marsh or fen vegetation very generally involves the assumption that the succession of communities follows from the reaction of the plants in producing a soil gradually emerging from the water and becoming progressively drier. Further, the zonation of communities round open water in these areas, that is their arrangement in space, is generally held to be controlled in the same way as the sequence of communities in time. This

<sup>1</sup> Godwin, H. and Bharucha, F. R., "Studies in the Ecology of Wicken Fen," Part II.

is made likely by the fact that in some cases the two series of communities, the spatial and the temporal are apparently identical. Probable as it may be that the ground level and water level relations are of fundamental significance, there is lacking any exact knowledge of the way in which their control is effective.

A first fact of significance is that control of vegetational distribution by the soil water level may be much more striking at one time of year than at another. It may be during a month of winter flooding that its effects are most marked (cf. Small on the fenlands of Lough Neagh) (2); it may be during the early growing season, or in the height of summer. In the first two cases it might be expected to operate through the varying resistance of different species to excess ground water, or deficient aeration, and in the latter case, with a low water table, it might possibly work through the varying resistance of plants to deficiency of soil water. Before it is possible to approach these questions it is necessary to get a fairly accurate idea of the general behaviour of the water table throughout the year and some idea of the causes underlying its fluctuations. As a first step towards this, an automatic water-level recorder was installed on the fen in the middle of "litter" vegetation. Its position is marked on the map of Fig. 19 as pit 17.

#### WATER-LEVEL RECORDER.

The apparatus is of a simple type, especially constructed to be weather-proof and insect-proof. On the latter account especially, the arm actuated by a rising and falling float does not enter the inner case of the recorder by a slot, but is attached to an axle which runs through bearings in the walls of the case, and which carries inside the case a pen writing on a drum. This is a modification of a thermograph made by Messrs Negretti and Zambra, and is supplied with a 28-day clockwork-driven drum. The float is a large glass bottle floating in a pit dug in the peat, and it carries a long vertical glass tube running through guides. This is connected by a suitable joint to the arm moving the recorder axle, and the arm can be varied in length so as to write in any of several different scales on the drum. Usually it was set so that 10 cm. rise or fall of the float was represented by 1.7 cm. on the record. The recorder is enclosed in a locked outer case and is carried on a platform fastened to four large stakes driven 4 to 5 ft. (1.2 to 1.5 m.) into the peat. The instrument is shown set up in Plate XXVII, Phot. 1. The instrument has been in use for two-and-a-half years and has proved quite satisfactory. The errors it allows are quite sufficiently small to be neglected for our purpose, and it is sensitive enough to give a very clear record of a daily change in level of less than 2 cm.

The curves of the rise and fall of the water level in the fen throughout the year (see Figs. 2 and 3) show features which can best be considered under the headings:

- (1) Effect of rainfall (precipitation).
- (2) Seasonal drift.
- (3) Rhythmical daily fluctuation.



Nevertheless these curves are also subject to the control of a factor scarcely deducible from their form, and yet of the utmost importance. This is the drainage system of the fen both as regards inflow of water and as regards its outflow; especially in the latter respect we shall see its significance. It tends to set the broad limits of the water-level movements and must be understood before the more detailed nature of the curves can be considered.

#### THE FEN DRAINAGE SYSTEM.

The separate levels of the fen drains in the neighbourhood of Wicken have been recorded carefully by Farren (3). The drains of Wicken Sedge Fen all communicate with Wicken Lode, which joins Burwell and Reach Lodes just above Upware (see Fig. 1). Here locks prevent the water in them from

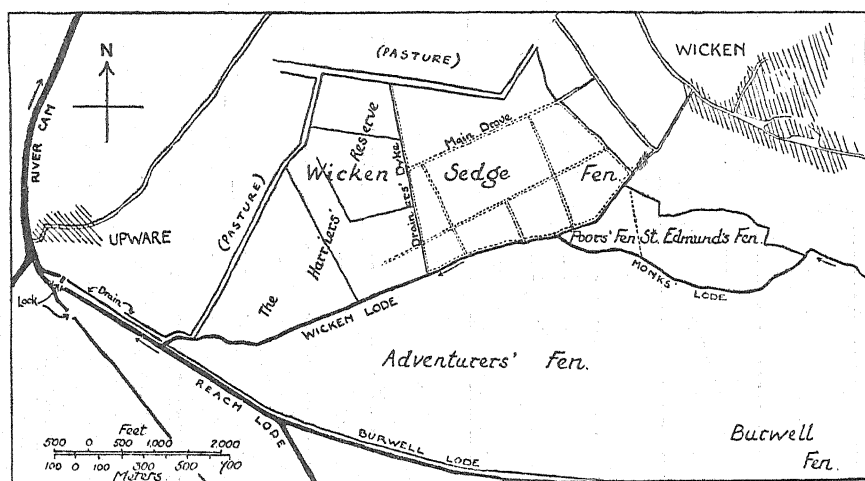


FIG. 1. Sketch-map of fens near Wicken, showing main drainage system, and in the eastern (open) part of Wicken Sedge Fen also the droves and paths.

flowing directly into the River Cam, which is usually a few feet lower in level. In the summer no water is allowed through the locks and the level may fall some inches below the overflow sluices in the gates, but in the winter, in order to keep cultivated land in the Burwell region unflooded as far as possible, the excess water is run off into the Cam, so long as that river is at a lower level, as it almost always is. The lock-keeper attempts to maintain the water level in the lodes at a mark fixed by the drainage authorities responsible for the lands involved. The fen lodes and drains are fed from three main sources: (1) direct rainfall on the fen, (2) direct drainage from the chalk escarpment lying to the South-east, (3) pumping of water into the fen drains from surrounding agricultural land, especially when the latter is flooded or in danger of being so.

Wicken Sedge Fen and its lodes lie at a level several feet above that of the surrounding agricultural land and the neighbouring fens, which are in different



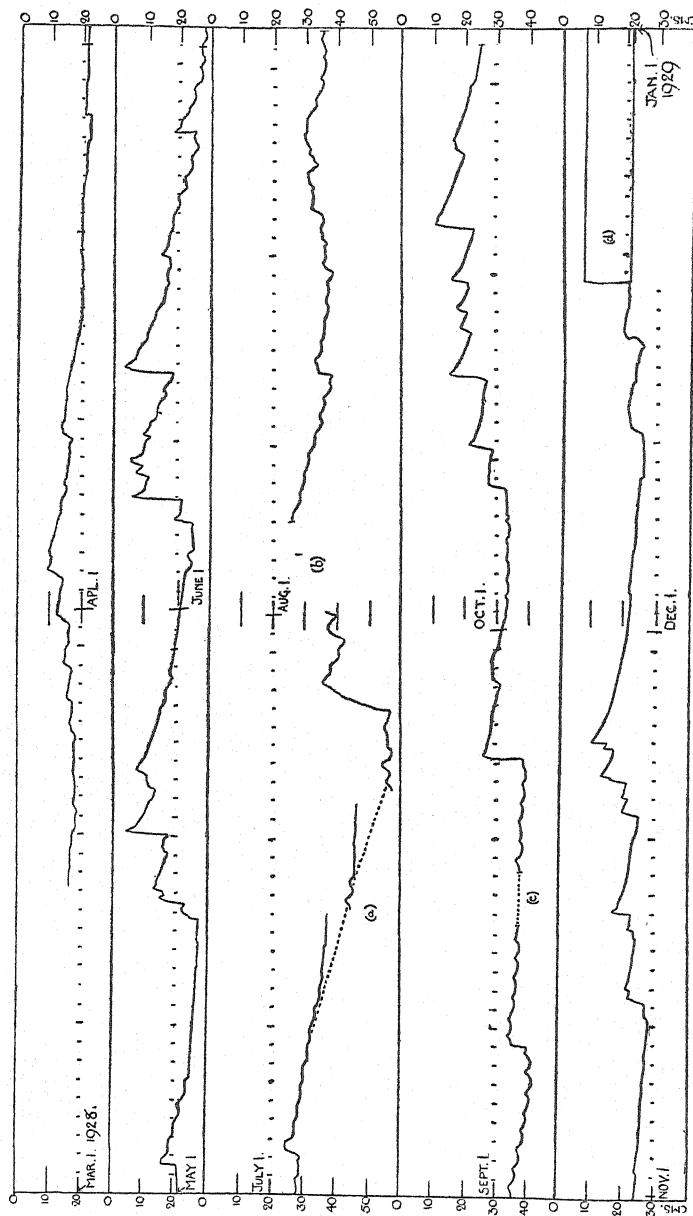


FIG. 2. Record of automatic water-level recorder from Mar. 17, 1928 to Jan. 1, 1929. The mark shown for each day represents noon. Average soil level is the line marked 0 cm. At (a) the pit had twice to be deepened as the water level was falling very rapidly and the dotted line represents the probable true fall of the water level. For (b) there is no record; at (c) the dotted line shows the probable level; and at (d) though there is no record through the clock having run down, the horizontal lines show the extreme limits of water level during this time; it is obtained from the range of travel of the pen on the stationary drum.

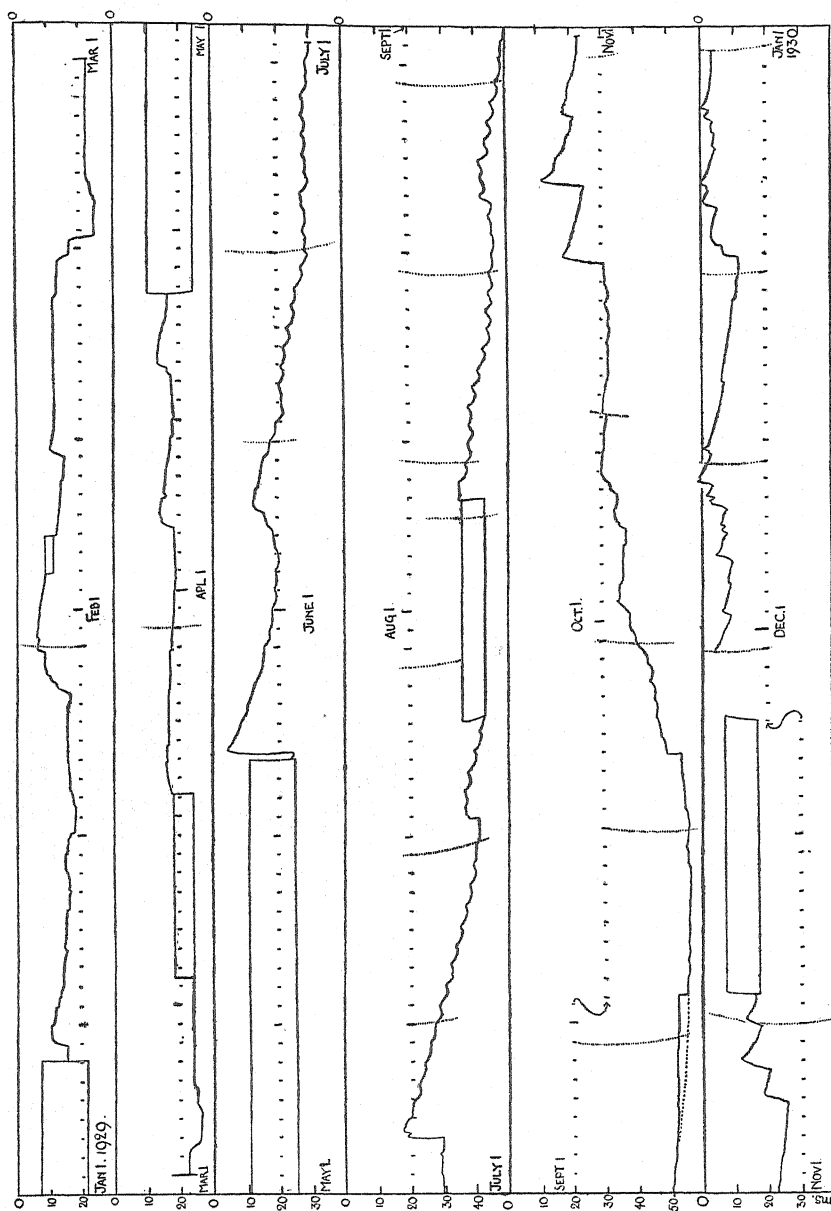


FIG. 3. Record of automatic water-level recorder from Jan. 1, 1929 to Jan. 1, 1930. The mark shown for each day represents noon and the curved dotted lines represent the arc of travel of the recorder pen. Each of the places where the record is shown by two parallel horizontal lines represents a time during which the recorder clock had run down (see explanation below Fig. 2).

stages of draining, drying-out and shrinkage. The Sedge Fen, within its border of lode banks strengthened with impervious gault clay, thus forms a large raised basin above the level of the surrounding land. The various sources of water supply to it are sufficient when combined with the controlled outflow at Upware, to keep the water level in it roughly constant through the year. It is locally believed that in wet winters it behaves as a large reservoir which takes the swollen volumes of water from the chalk hills, and so saves the surrounding country from flooding in any but specially severe conditions.

These are the circumstances underlying the rather unexpected occurrence of a relic of the British fenlands, still wet enough to carry an extensive fen vegetation, and yet at a definitely higher level than surrounding cultivated or semi-cultivated land.

That little further reference should be possible in this paper to the effect of running off water at Upware, or to pumping from the land around, is to be excused on the grounds of difficulty of getting information accurately and continuously of such activities, and of the relatively greater importance of devoting time to measuring the actual water-level changes in the fen itself (since it is these that directly affect the vegetation there) rather than to devoting time to finding the causes of the water-level changes themselves. Further, although the lock control tends to prevent the rise of the water table above a certain level, it can only diminish the rate of fall by permitting no drainage from the fen and cannot set a limit to the fall as it can to the rise. Thus though the winter water level in the fen may be due to control by the lock-keeper at Upware, in the summer other factors will be in control<sup>1</sup>. Pumping also only takes place in the winter, when its effect is nullified by the lock control at Upware.

#### RAINFALL.

The effect of rainfall on the water level is quite definite, as can be seen from the diagram (Fig. 4) in which both are plotted on the same time scale. The rainfall is that at Fordham<sup>2</sup>, a village 4.5 miles (7.2 km.) away in an easterly direction, which stands on the low ridge of land round the fens. Its rainfall record will probably not differ greatly from that of the fen itself. The rainfall is given as the total fall per day, and it will be seen that on each day of heavy rainfall the water level on the fen shows a sudden steep rise. It is important to notice how extremely rapid this rise is; it is often complete in two or three hours, which period is presumably the duration of the heavy rain responsible for the rise. This fact suggests that the rise is due directly to the effect of rain falling on the fen itself, and not to the rise of water level in the lodes and drains caused by water draining in from the chalk hills. It has been verified by

<sup>1</sup> In the summer of 1929, according to the lock-keeper, for three consecutive months no water at all was run out of the lodes.

<sup>2</sup> I am indebted for these rainfall data to Mr W. V. Bloom, London House, Fordham, who has been responsible for collecting them.

observation in heavy thunderstorms that the water level in the fen does indeed rise immediately the rain begins.

It is interesting to compare the amount of rainfall per day with the magnitude of the rise which follows it, and on the graph given in Fig. 4 the values are as follows:

	Oct. 17	Oct. 20	Oct. 24	Oct. 28	Nov. 5	Nov. 6	Nov. 7	Nov. 10
Rainfall (cm.)	1.2	1.74	1.45	0.45	0.17	0.6	1.03	0.47
Rise (cm.)	15	13	14	3	—	7	9	4
Ratio $\frac{\text{rise}}{\text{rainfall}}$	12	8	10	7	—	12	9	8

Thus, with the exception of November 5, on which day it is quite possible that no rain fell on the fen, every cm. of rainfall caused a rise in water level of from 7 to 12 cm. This was clearly because the rain was not falling into an open vessel but was filling up the air-spaces in the soil. Measurements show that the pore space of the upper 20 cm. of the peat of the fen (which is what we are now

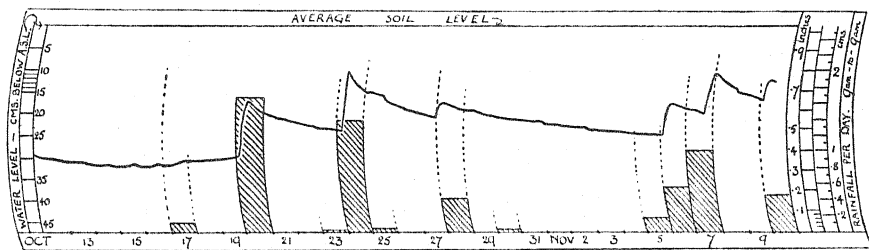


FIG. 4. Diagram to show the variation in level of the water table in Wicken Fen during part of October and November, 1929, and the corresponding daily rainfall.

dealing with) amounts to about 10 per cent. of the volume of the soil. This, neglecting drainage away during rainfall, would give a value for the ratio  $\frac{\text{rise}}{\text{rainfall}}$  which corresponds to the values observed.

It will be noticed that following each sudden rise in the water-level curve there is a fall towards a lower level, rapid at first, but always becoming less rapid. Whether the curve would become flat it is scarcely possible to say, but its form in any case strongly suggests that it represents the drainage of water from the fen into the drains and lodes (and possibly through the locks into the Cam) after a period of rain. The final level in the lodes will naturally not always be the same, as can be seen from Fig. 4. The rainfall records or the year's water-level records (Fig. 3) show that the rains of October and November indicated in Fig. 4 were the first heavy rains for several weeks and it is interesting to note that the new level to which the water-level curve falls after this period of fairly heavy rainfall, is much higher than the old one. A more accurate expression of this fact is given in Fig. 5.

In this figure is shown the fall of the water level in the fen after rain at different times during the autumn of 1929. In each case it is plotted so that

zero time is the time when a heavy rainfall has just ceased. From mid-October to December it seems clear that the water level in the lodes has risen about 20 cm. This is apparently the level to which the fen water level sinks after a temporary rise due to rain<sup>1</sup>.

By reference to the rainfall data through the year it is easy to see that the water level on the fen responds throughout the year to rainfall in the manner illustrated by the foregoing example.

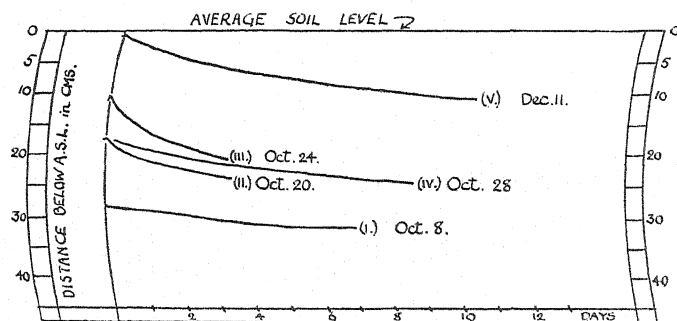


FIG. 5. Diagram to show the water level during drainage into lodes from the fen after periods of rainfall, October to December, 1929. The Roman numerals in brackets show the sequence of the five curves and each date is the period when the cessation of rainfall allowed the water level to fall by drainage into the lodes. There is from October to December a rise in the level in the lodes.

#### SEASONAL DRIFT.

In Figs. 6 and 7 may be seen plotted the half-monthly averages for the water level during the years 1928 and 1929; these are directly derived from the original records illustrated in Figs. 2 and 3. A strong similarity in general behaviour for the 2 years is evident. We may generalise by saying that from the end of October to the beginning of June the water level is high, it is less than 20 cm. below the average soil level, and indeed may for some time be less than 10 cm. below it; whilst during the five months from June to October much lower values prevail—average half-monthly values of more than 30 cm. lasting for about 3 months, and much lower values being prevalent for a long period in 1929. The original records show that for 6 or 7 days in July 1928, and for 20 days in August–September, 1929, the water level was more than 50 cm. below A.S.L. (Average Soil Level). The beginning or middle of June in each

<sup>1</sup> It might be thought that the recorder pit was being filled up by surface drainage from the peat round it during rainfall and afterwards slowly came into equilibrium with it, thus giving the typical form to the curves during rainfall and not at all representing the real behaviour of the water level in the peat of the fen as a whole. This is made unlikely by the fact that the peat is extremely porous, so that after a hole has been dug in it, it fills with water very rapidly, the level coming after only 2 or 3 hours to within 0.5 cm. of its final value, whereas the continued fall after rain may last several days. Expressed in another way we may say that if the level in a pit in the peat is raised a few centimetres by filling it with water from a bucket, the level falls again much more rapidly than it is seen to do after rainfall.

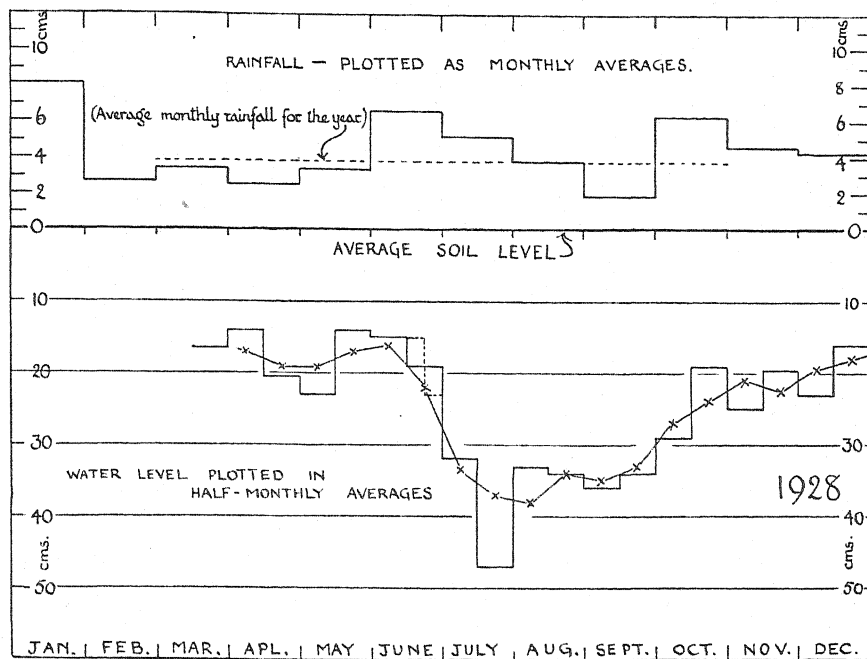


FIG. 6. Diagram to show, for 1928, the yearly course of the fen water level as given by recorder in pit 17, and corresponding rainfall.

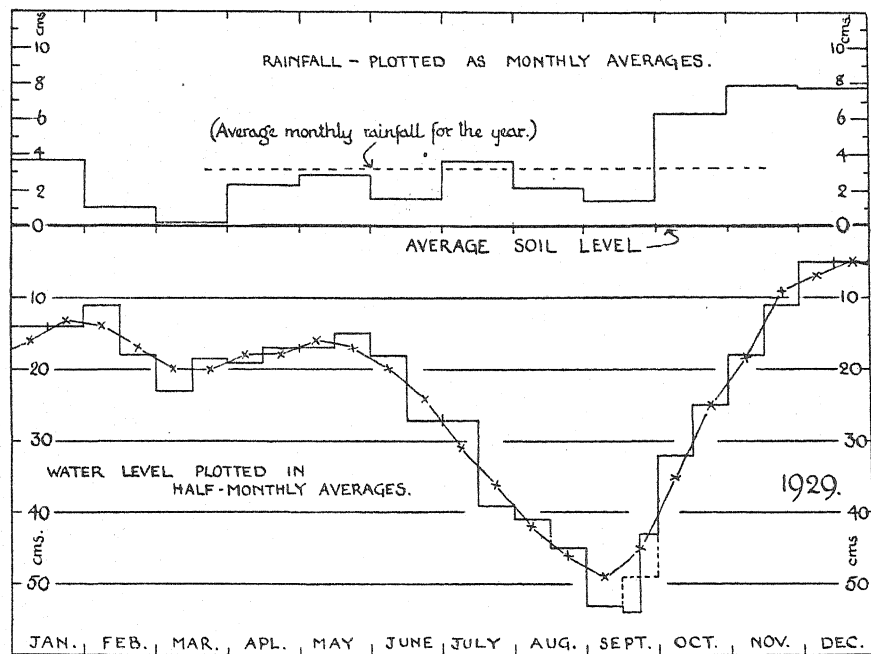


FIG. 7. Diagram to show, for 1929, the yearly course of the fen water level as given by recorder in pit 17, and corresponding rainfall.



year shows the commencement of a very sharply marked and rapid fall in the water level, which continues until August or even September. In September a rise sets in which continues until the high winter levels of December and January have been reached.

Two facts are most striking about this behaviour: (1) that the period of low water level should coincide so sharply in time for both years, and especially the marked initial fall in June; (2) that neither fall nor subsequent rise seem to be related to the rainfall figures. The figures show that during the rapid fall in June and July the fen was receiving at least the average monthly rainfall, indeed the July rainfall for 1929, and both June and July rainfall for 1928 were all above the average monthly rainfall for the year. Similarly the rise of water level begins quite definitely in September when the monthly rainfall in both

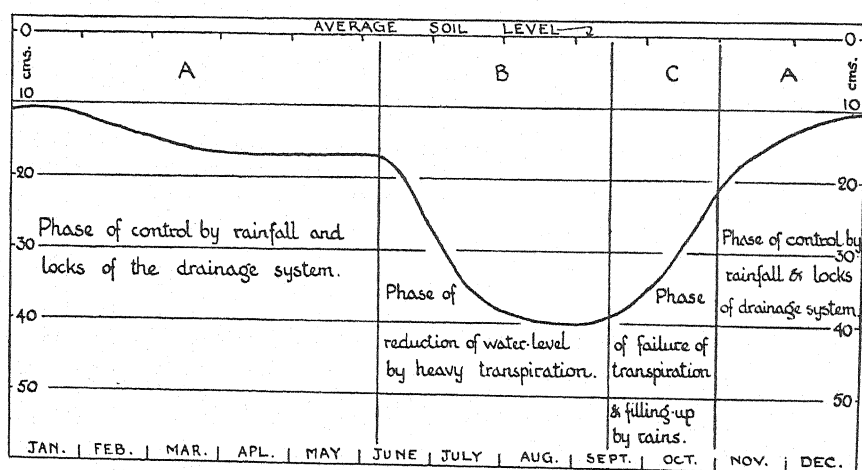


FIG. 8. Diagram to show the yearly drift of ground water-level behaviour in the fen.

1928 and 1929 was only about half the average monthly rainfall of the year, and certainly lower than in the preceding months of falling and constantly low water level.

It seems clear that diminished rainfall is not responsible for the lower summer water levels, and we have the direct evidence of the lock-keeper that his locks are shut all through this period. The possibility suggests itself that it is simply an expression of transpiration of the fen vegetation, and this indeed is the conclusion to which further evidence points.

(1) The period of rapid fall in water level takes place when the fen vegetation is growing most rapidly, i.e. the transpiration surface is increasing very swiftly. The period of subsequent rise in the water table again corresponds with the yellowing and dying-off of the fen vegetation.

(2) Examination of the direct water level record for the year (Figs. 2 and 3) will show that about June 1 there first becomes evident a definite daily

periodicity which involves a rapid fall of level during the middle of the day and a partial recovery at night. This is a phenomenon which becomes very marked during July and August, and it disappears again by the end of September. Its occurrence thus coincides with the period of low water level. This daily fluctuation in level is almost certainly due to the transpiration of the fen vegetation. Where the periodicity is strongly marked the fall in level induced each day by transpiration is only partly compensated for by recovery at night, so that a progressive lowering of the fen water level goes on. When the vegetation begins to die off and the daily fall in level becomes less marked, as at the end of

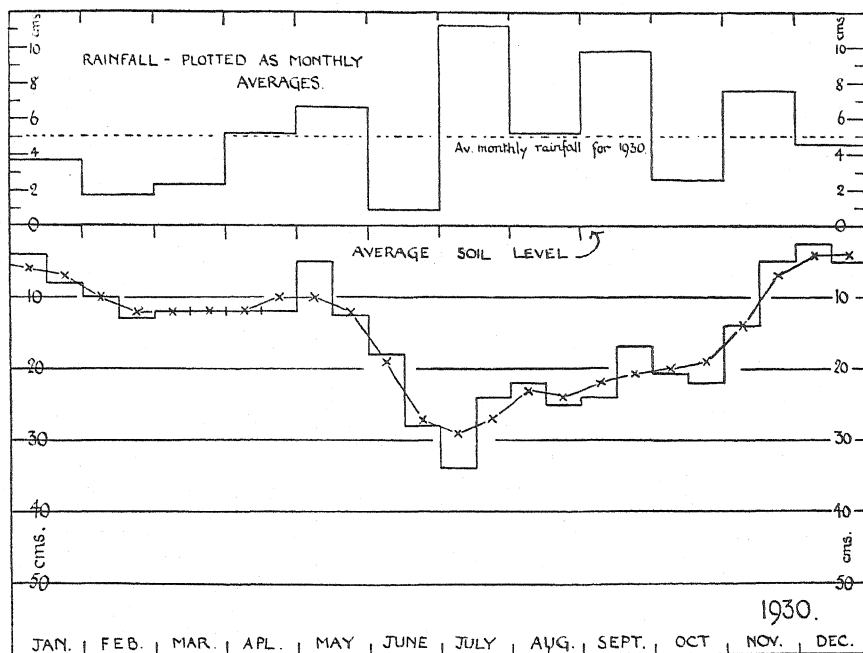


FIG. 9. Diagram to show, for 1930, the yearly course of the fen water level as given by the recorder in pit 17, and the corresponding rainfall.

September (see Figs. 2 and 3), the inflow of water from the lodes more than balances the transpiration loss, and even in absence of rainfall the fen water level will rise. Then the rains of October and November will accelerate the filling up of the fen. The situation may be summed up by Fig. 8.

It expresses the sequence of three phases:

- A. November-June. Phase of control by rainfall and locks of drainage system.
- B. June-July-August. Phase of reduction of water level by heavy transpiration, and of maintained low levels.
- C. September-October. Phase of failure of transpiration and filling up of the fen by autumn rains.

This picture is both confirmed and elaborated by the data for 1930 which are set out in Fig. 9 and which are compared with the data for 1928 and 1929 in Fig. 10. These figures show the same winter phase of high water level as before and the sudden incidence of falling levels at the beginning of June. The water-level curve for 1930 differs from those of the two preceding years in the short duration and small extent of the fall in level. This is certainly due to the exceptionally heavy rainfall of the latter half of July, 1930. It was so great that the fen water table rose considerably despite high summer transpiration values.

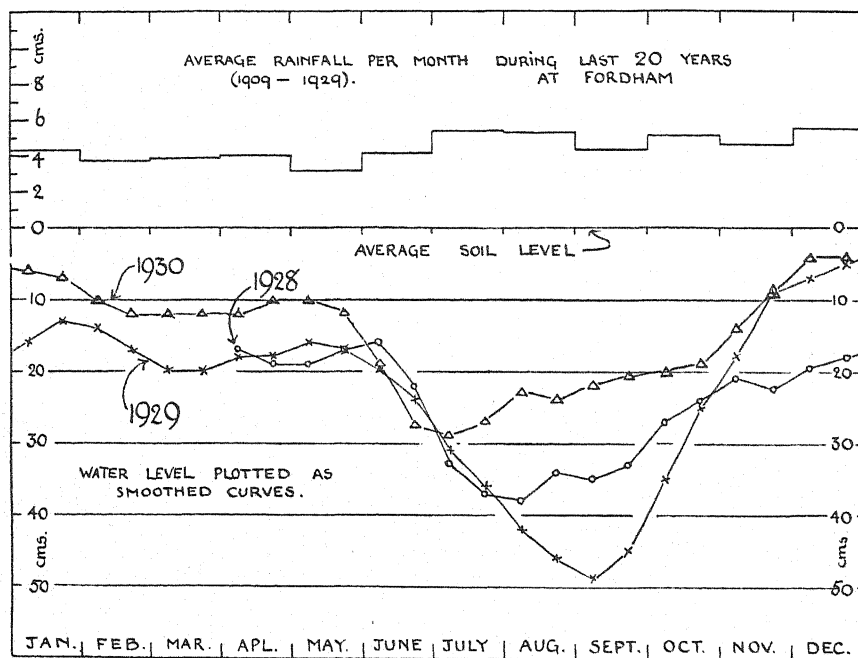


FIG. 10. Diagram to show the yearly course of the water level in the recorder pit in the fen from March, 1928 to March, 1930, and for comparison the average monthly rainfall over the last forty years.

In Fig. 10 it will be seen that 1929, 1928 and 1930 form a series in regard to the lowness of the summer water table and the persistence of low values. This is almost certainly related to the summer rainfall as we see from the values for total rainfall during July and August:

1928	11.0 cm.
1929	5.8 cm.
1930	18.4 cm.

Since the average total rainfall for these 2 months over the last 20 years at the same station has been 10.5 cm., we may take the curves for 1928, 1929 and 1930 as representing a fairly full range of behaviour for the fen, and in their

opposing effects on summer water levels we can assume that transpiration usually predominates over rainfall. We may thus say of the phases of water level that the uncertainty involved in this schema lies chiefly in its applicability to the fen as a whole. The continuously recording instrument is set up in "litter," which is vegetation dominated by *Molinia caerulea* but containing *Juncus obtusiflorus* and *Carex panicea* abundantly. How far may results from this one situation be applied to the rest of the fen, especially in view of the fact that this comprises areas of very different types of vegetation, some such as "carr"<sup>1</sup> which may develop at the same period as *Molinia*, but may transpire at a far greater rate per unit area of fen, and some, such as mixed or pure sedge<sup>1</sup>, in which the evergreen *Cladium mariscus* is dominant and may be expected to transpire all the year round, though more at some times than others? The answers to these questions cannot be altogether complete without similar continuous yearly records being made at the same time in different parts of the fen. Nevertheless we can be assured that in a broad sense the scheme outlined does apply to the whole fen, by reference to water-level measurements taken in a large number of pits dug in different parts of the fen (Fig. 19). Readings were made of all the pits as nearly as possible simultaneously and this was repeated on several days at different times of year (see Part II of this series).

#### DAILY FLUCTUATION OF WATER LEVEL.

As already mentioned, from about June to September the water-level records show a marked daily periodicity, the nature of which can be seen from

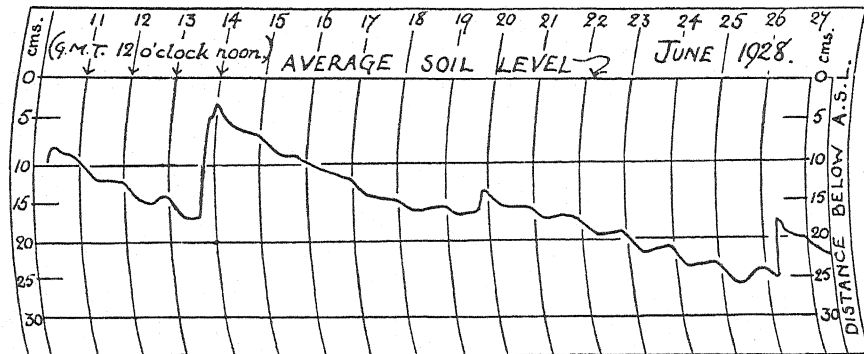


FIG. 11. Diagram of the water-level record itself at the end of June, 1928, to show the daily fluctuation in level.

Fig. 11, which shows a section of the record about two-thirds of its real size. This concerns the period of year when the periodicity is becoming most definite (Phase B), and in the latter part of the month it is clear that every day there is a rapid fall for about 8 or 10 hours followed by a longer period of slower rise. The recovery in each case is only about one-third or one-fourth of the

<sup>1</sup> For description of these communities see (1).

previous fall, so that apart from the rainfall (indicated by the sudden peaks) the graph shows a continued fall in the water level. It appeared from the recorder graphs that the fall in level took place each day between about 9 a.m. and 6 p.m., and that the distance involved was about 3 cm. Allowing a recovery of 1 cm. each night this gives an average fall through several days of about 2 cm. a day, which is quite considerable. The scale of the graphs was too small for them to yield further information about the daily periodicity and so in August, 1929, by a long light balanced lever attached to the float of the water-level recorder, an index of very much greater sensitiveness was obtained

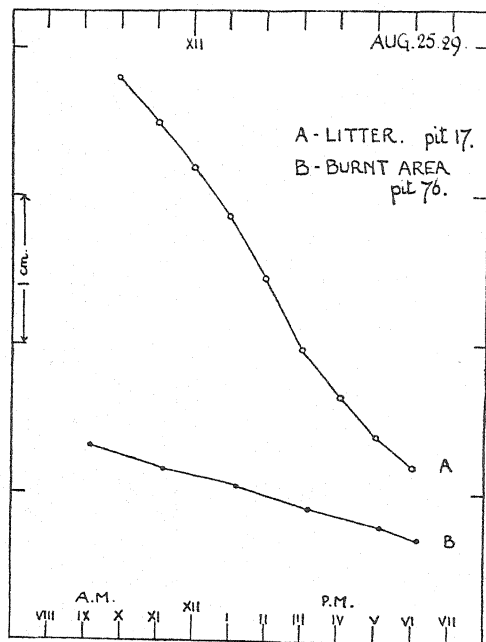


FIG. 12. Diagram to show the daily fall in the water level in pits dug (A) in litter, and (B) in the burnt area.

(see Plate XXVII, Phot. 2). Similar apparatus with a float moving a long lever arm was also placed in two other places in the fen—(a) in the middle of a large area accidentally burned bare 10 days before<sup>1</sup>, (b) in developing carr. In no case was the apparatus self-recording, which set a limit to its value. Records were made of the water level throughout two successive days, August 25 and 26, and the results are shown plotted in Figs. 12 and 13. On both days there was clear and bright sunshine with a very light breeze; both were hot days, especially August 26, though no temperature records were taken. There was mist all over the fen at 7 a.m. (Greenwich mean time) and dew remaining on all the

<sup>1</sup> By accident on August 15 about 700 acres (280 hectares) of the fen were burned and in this area, although all plant parts in the wet peat survived, everything above the surface was consumed.

vegetation till after 8 a.m. The level in the litter vegetation (the water-level recorder pit) was seen on the first day (Fig. 12) to fall continuously from the first reading at 10 a.m. (G.M.T.) until the last reading at 6 p.m. On the second day, more extended readings showed that until 9 a.m. the water level was still rising (as it had been doing all night, having recovered at 7 a.m. 1.5 cm. from the last reading of the previous day). After 9 a.m. the level fell continuously, but between 7.10 p.m. and 7.30 p.m. the fall had slackened off almost to nothing, and it appeared probable that the slow evening recovery was beginning. The data were just good enough to allow the plotting of the hourly rates of fall of

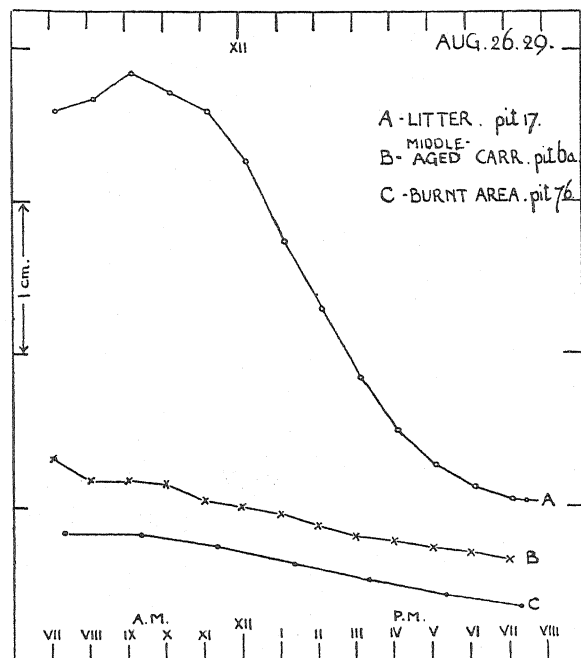


FIG. 13. Diagram to show the daily fall in the water level in pits dug in the middle of (A) litter, (B) middle-aged carr, (C) burnt area.

the water level, and these are given in Fig. 14. It will be seen that the curves for both days coincide quite closely, especially in respect of the period of maximum rate of fall, which lies between noon and 3 p.m., and in respect of the slackening of the rate of fall which, beginning about 3 p.m., will clearly reach zero value about 7.30 p.m. The commencement of the fall in water level is not quite so clear, but it apparently began about 9 a.m. and increased in rate till noon. The results given by the sensitive apparatus thus confirm the presence of a clear-cut daily phenomenon in a way not possible with the less sensitive self-recording instrument. We have already seen reason to think that this daily fall is a transpiration effect. The ground can indeed evaporate little moisture directly to the air, closely covered as it is with vegetation, but as a check on the



effect of the vegetation in producing the daily fall in water level, records were made in a pit in the middle of the area from which all surface growth had been cleared by fire 10 days earlier. The wet peat surface was quite exposed to evaporation save for a thin surface layer of plant ash still dry. In Figs. 12 and 13 it will be seen that the water level in this case shows a far slower and gradual fall throughout the day (falling 6 mm. as against 26 mm. in the litter on August 25, and 5 mm. as against 28 mm. on August 26). In the night following August 25 the level in the burnt area pit recovered about 1 mm. It does not follow, of course, that the daily fall in this area need be due to direct evaporation from the soil; it might equally well be due to the effect of neighbouring unburnt fen draining water from it, though in the light of later drainage observation this is not very likely.

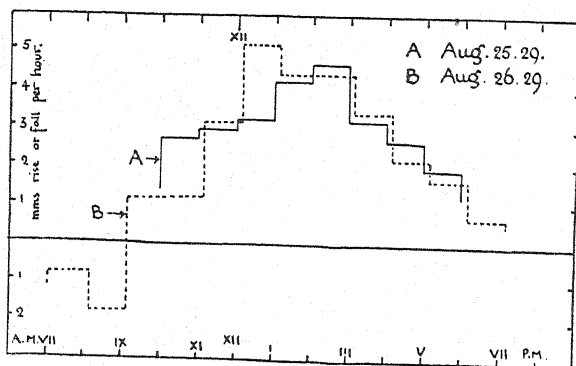


FIG. 14. Diagram to show the rate of rise or fall of the water table throughout the day in pit 17 in litter vegetation.

#### INSERT PHYTOMETER EXPERIMENT.

The analysis of the water-level recorder curves was carried a stage further by the employment of what we may call for convenience an "insert phytometer" apparatus. This was a large water-tight box, containing growing "litter" vegetation, and so contrived that water loss from the box could be measured at any time. Its construction is shown in Fig. 15. It was 3 ft. (91 cm.) deep (i.e. deeper than the usual root penetration of fen plants) and 1 ft. (30 cm.) square. It was made of tinned sheet iron and when completed was painted with water-proof varnish which was afterwards washed down with water several times. A few centimetres from the base and in the middle of one side a tap gave communication between the tin and the fen outside. The tap both inside and out was closed by a small cylindrical cage of perforated metal to prevent large pieces of peat from choking the tap. By a long key reaching above the upper level of the tin the tap could be opened or closed whilst the vessel was undisturbed, embedded to soil level. On the face of the tin opposite to the tap and extending the whole length of the vessel were soldered two vertical metal tubes more or less semicircular in section. Of these, one (a) was perforated with

holes at intervals all up the curved outward wall. The other (*b*) was similarly perforated on the flat wall of the vessel itself. Each tube was closed at the base so that tube *b* was effectively part of the big vessel; *a* was sealed off completely from it, though attached to it. Each tube ended at the top in a suitable neck which could be closed by a stopper, and between the two necks the lip of the tin carried a metal support rod. When embedded in the peat the two holes behaved in this way: tube *a* behaved as a tiny narrow well in communication

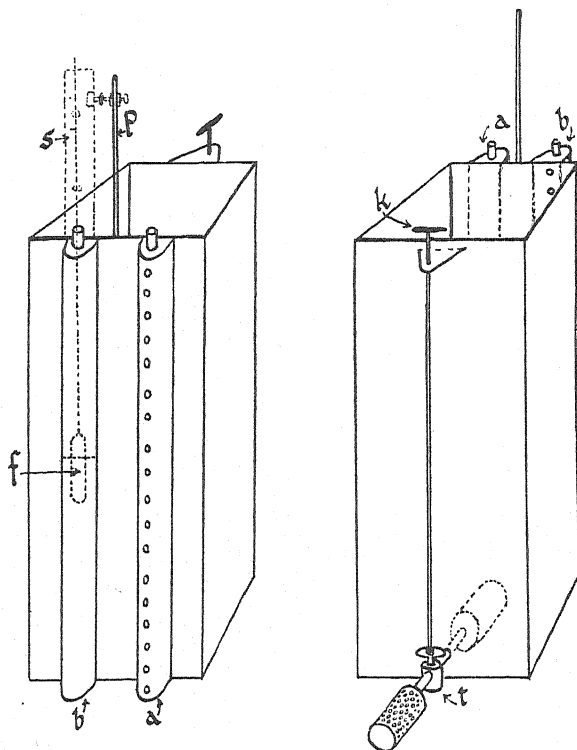


FIG. 15. Insert phytometer apparatus. *a* and *b* are narrow wells each containing a float (shown dotted at *f*), an extension of which moves over the scale *s*. *a* is open to the fen, *b* to the inside of the vessel, *t* is a tap controlling communication between the fen and the inside of the phytometer vessel, *k* is control key at peat surface, *p* support.

with the fen outside, and tube *b* as a similar well in communication with the peat within the tin. In each tube was placed a glass float carrying a delicate glass pointer emerging through the neck and running through guides against a vertical millimetre scale. By this means the exact rise and fall of the level in the vessel could be followed in the one tube and those in the surrounding fen at the same time in the other. (See Plate XXVII, Phot. 3.)

The first readings with the apparatus were made in July, 1930. In the same year a deep pit was dug in litter a few metres from the water-level recorder pit

and a large block of peat with representative living vegetation was transferred as a whole to the tin vessel which it had been cut to fit, the vessel was sunk in the pit so that the lip of it came just to the peat level, and the rest of the pit was filled in and replanted with the top sods of the original vegetation. Within a few months traces of disturbances were not at all evident in the growth of the vegetation.

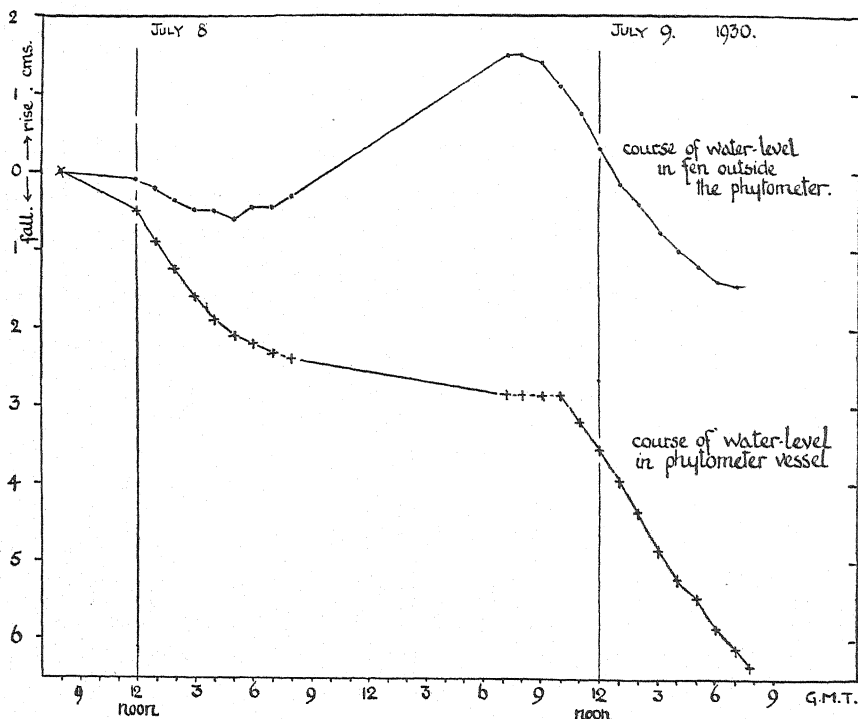


FIG. 16. Insert phytometer experiment of July 8 and 9, 1930, showing daily variation of water level in the two wells of the phytometer apparatus.

During the establishment of the plants in the phytometer the tap connecting the vessel with the fen outside was left open so that the phytometer plants were subject to just the same water-level conditions as those in the fen around. That this was so was checked by the fact that the levels in both side tubes remained the same during this time.

On July 8 at 8 a.m. (G.M.T.) the tap was closed, and from that time the phytometer vessel was essentially a transpiration vessel independent of water-level changes in the rest of the fen. Changes in it were followed in tube *a*, changes in the fen water levels in tube *b*.

#### Results.

On July 8 at 8 a.m. (G.M.T.) the floats in both tubes were found to give the same zero reading and the tap was then closed. The next reading was then taken

at noon, and thereafter readings were taken every hour till 8 p.m.; the next morning readings recommenced at 7 a.m. and were continued hourly until 8 p.m. The results are shown in Fig. 16. It is clear that both in the fen and phytometer there is a pronounced fall in the water level during the day, but whereas the level remains constant or falls slightly at night in the phytometer, it rises considerably in the fen. The following conclusions may be drawn from the results.

#### *Conclusions.*

Transpiration in the phytometer will bring about a daily fall in water level of the same order of magnitude and the same character as the daily fall evident in records of the fen levels. In these latter the fall is then presumably transpiration also.

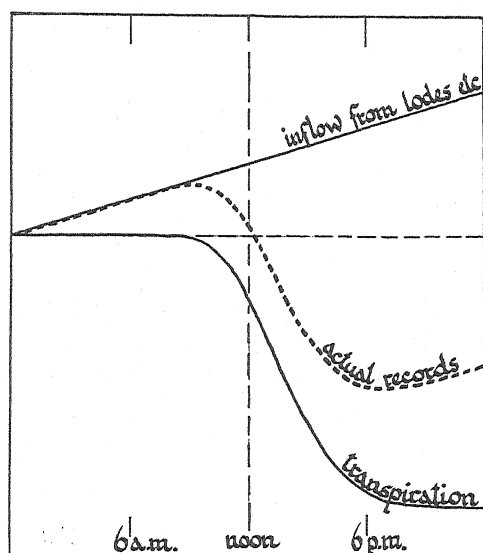


FIG. 17. Diagram to show factors in the daily periodicity of water-level movements in the water-level records (pit 17).

Practically all the significant differences between the fall in level in the phytometer and in the fen around can be explained on the basis of a continual drainage into the fen at that point of water from neighbouring drains, etc. This is evident as a rise of about 2 mm. per hour during the night, and if a correction of this magnitude is applied to the water-level curve during the day as well as the night, so as to find the probable fall of level due only to transpiration from the fen, a curve is obtained very like that of the phytometer.

Thus for the recorder pit in the litter the explanation of the daily fluctuation in the form of the water-level curve is to be found in the interaction of (a) transpiration lowering the level, (b) drainage in from the lodes raising it: (b) is

continuous through the 24 hours, but (a) is limited to the day and may vary also from day to day in magnitude.

This may be expressed by Fig. 17.

#### SIMULTANEOUS WATER-LEVEL RECORDS.

The phytometer experiment left little doubt that in the curves of the permanent water-level recorder the daily periodicity during the summer was due to (a) plant transpiration and (b) drainage inwards from lodes and dykes. It was not, however, entirely clear that the drainage channels might not be showing also a marked daily periodicity in level, due to some cause outside the fen, and that this might not be responsible to some extent for the daily periodicity in the water-level curves of the recorder pit. The channels might, on the other hand, be showing a daily periodicity in level which might be a *result* of the changes in level in the fen as a whole. The problem of the nature of

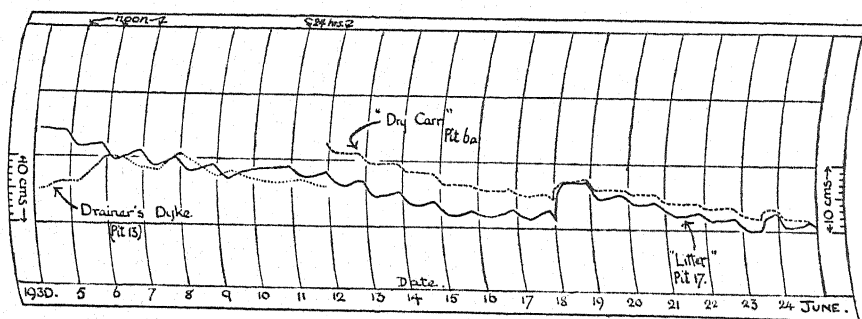


FIG. 18. Water-level records obtained by automatic recorders working simultaneously in pit 13 and pit 17, or in pit 6a and pit 17.

water-level behaviour in the drainage channels was attacked by placing in a neighbouring dyke (Drainer's Dyke) a second water-level recorder like the first in all respects save that it was made readily portable to various permanent platforms set up beside pits in different parts of the fen. A few days' simultaneous recording of the levels in Drainer's Dyke and in the permanent recorder pit situated 50 m. away in the litter vegetation, sufficed to give conclusive results. The curves for the two recorders are shown together in Fig. 18.

#### (a) Pit 17 in Litter and Drainer's Dyke.

The weather from June 4 to 12 was fine and hot. The water level in the litter showed a continuous fall for five days and then stayed more or less flat, although on every day save one the rapid fall due to transpiration was evident, with marked recovery at night. In the dyke record there was no evidence at all of a fall by day and a rise by night, or of any large periodic rise or fall, so that the cause of the periodicity in the litter cannot have been the changing dyke levels.

In the dyke there seems an ill-expressed fluctuation which is difficult to relate to the periodicity of changes of level in the litter. The peculiar general form of the dyke curve is due to the fact that weeds were cut early in June in

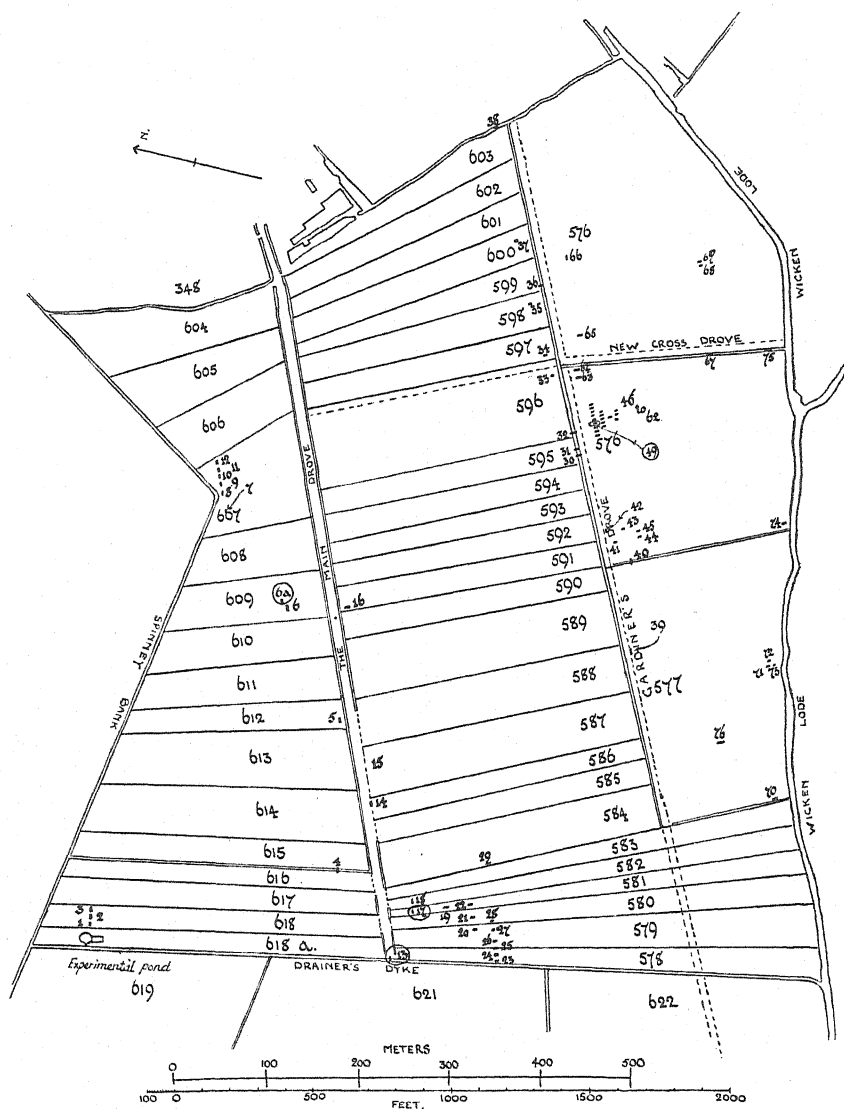


FIG. 19. Map of Wicken Sedge Fen showing the position of the water-level pits (numbered 1 to 76) in relation to droves, dykes and the strips of land once under separate ownership. The pits indicated by ringed numbers (6a, 13, 17 and 49) are those used with special water-level recording apparatus (see text).

Monk's Lode (see Fig. 1), but those in Wicken Lode were uncut. The released water could not get away, so that it flooded all the village end of the Sedge Fen



and was responsible for the rise in level of Drainer's Dyke between June 4 and 8, and the maintenance of the high level afterwards.

It is noteworthy how little the form of the dyke curve is reflected in that of the litter; the latter seems to be falling continuously under the influence of a high daily transpiration which cannot be compensated for by drainage in from the dyke. We can apparently say with safety that during June transpiration in litter is so great that except very near lodes and dykes it removes more water than can flow in from such drainage channels. Naturally the rate of drainage into any part of the fen is controlled by the distance from drainage channels and by the difference in height of the water table in the two places.

The foregoing results accord with the general system of explanation given earlier.

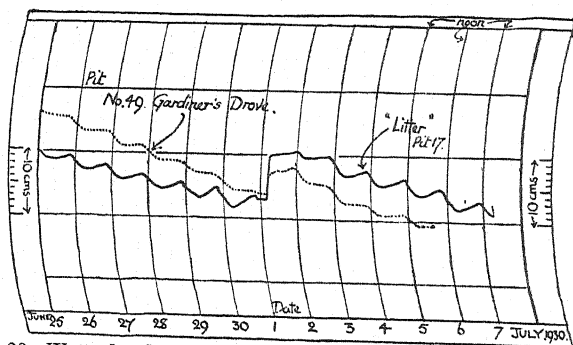


FIG. 20. Water-level records obtained by automatic recorders working simultaneously in pits 49 and 17.

(b) *Pit 17, in litter compared with pits 6 a and 49.*

If the recovery every night of the water level in the water-level recorder pit 17 is really due to inflow of water from Drainer's Dyke, as we have had very strong evidence to show, then pits much farther distant from drainage channels, whilst showing a daily fall in level due to transpiration should show at night a practically flat curve; they should, in effect, show a curve like that for the insert phytometer. When the portable recorder was placed in either pit 6 a or in pit 49 (the positions of which can be seen on the map, Fig. 19, to be a long way from open drains), the records were at once clearly evident as of this expected type (see Figs. 18 and 20).

The true relative heights of the water table in the pits 6 a and 49 are considered in Part II of this series; they are not indicated by Figures 18 and 20.

MAGNITUDE OF TRANSPIRATION BY THE FEN VEGETATION.

In the automatic recorder records, the phytometer results, and the delicate level indicator results we have ample material for rough estimates of the rate of loss of water from the litter vegetation of the fen, and we have material for comparison of one type of vegetation with another.

*Litter vegetation.*

If we take the experiment of August, 1929, as typical of the true midsummer conditions, we can use a mean value of 2.7 cm. for the fall in level between 9 a.m. and 7 p.m. The soil pore space is about 10 per cent., so that the water loss per square metre of litter will be 2700 c.c., and if we remember that during the whole 24 hours water has been draining in from the dykes at about one-quarter of this rate, we get a value of 3325 c.c., or over 330 c.c. per hour for the real transpiration rate. To make this good every day a rainfall of 3.4 mm. would, of course, be needed, which corresponds to a yearly rainfall of 124 cm. as against the Fordham record of 53 cm. for 1928 and 41.5 cm. for 1929. The common inadequacy of the June, July, August and September rainfall to cope with such high transpiration, and the slow rate of the drainage into the fen from the lodes account for the prevalent low water-levels during these months.

If other data are taken as the basis for calculation different figures of the same order will be obtained. Thus from the phytometer experiment the fall during the day of July 9th, 1930, was 3 cm. and if the previous night's recovery is used as a basis, about 2 cm. must be allowed for inflow from the lode between 8 a.m. and 8 p.m. Thus the fall during that day was 5 cm., corresponding with a transpiration of 5000 c.c. per square metre for the day, and over 400 c.c. per square metre per hour.

The recorder graphs yield similar data. Thus for the 12 days beginning July 1st, 1930, the average daily fall was about 2.4 cm., and the average rate of recovery such as to raise this figure to about 3.2 cm. for the fall due to transpiration alone. This corresponds with a loss of 3200 c.c. per square metre during the day. The recorder graphs (Figs. 2 and 3) show that these figures are fairly representative of the transpiration rate during the summer months.

*Burnt areas and carr.*

The movable water-level recorder was kept for a time at pit 6 a, in middle-aged carr of *Rhamnus frangula*<sup>1</sup>, and for a longer period at pit 49 in vegetation growing up during the eleven months since the fire in August, 1929. As there is no significant recovery in level at night in either of these places the total fall in level is attributable to transpiration, which we may compare in magnitude with that going on at the same time in the litter round the water-level recorder pit. The roughly worked out values are given in the table on p. 472.

The range of values shown between different communities is quite striking and the readings taken over several days are not likely to be anything but typical values for fine English summer days.

The transpiration value for the carr is apparently less than half that of the litter, and not a great deal more than that of completely bared ground. The

<sup>1</sup> For description of this community see (1).

vegetation of 11 months' growth after the fire (pit 49) shows transpiration values of about half those of the litter, and as it develops further this value may rise.

Date	Fall in water level due to transpiration*	
June 12 to June 15, 1930	Litter (pit 17) 4.1 cm. per day	Carr (pit 6 a) 1.6 cm. per day
June 26 to June 29, 1930	Litter (pit 17) 4.5 cm. per day	Young mixed vegetation (pit 49)† 2.0 cm. per day
June 19 to June 23, 1930	Litter (pit 17) 2.1 cm. per day	Carr (pit 6 a) 1.0 cm. per day
August 26, 1929 (sensitive level recorder)	Litter (pit 17) c. 3.5 cm. per day	Carr (pit 6 a) c. 0.7 cm. per day
June 25 to July 15, 1930	Litter (pit 17) 3.3 cm. per day	Young mixed vegetation (pit 49)† 1.6 cm. per day
August 25, 1929	Litter (pit 17) c. 3.5 cm. per day	Cleared by fire 10 days before (pit 76) 0.6 cm. per day
August 26, 1929	Litter (pit 17) 3.5 cm. per day	Cleared by fire 11 days before (pit 76) 0.5 cm. per day

\* Varying values for percentage pore space in the peat would invalidate these figures as indices to relative transpiration rates, but measurements have never shown substantial variation in the pore space figures.

† Pit 49 is in an area of ridge and furrow ground carrying pure sedge and stages of bush colonisation. This was burned clear in August, 1929, and at the date of the reading carried vegetation of 11 months' growth.

These varying transpiration values for different plant communities may be expected to have pronounced secondary effects upon the summer form of the fen water table, which will tend to be depressed below communities such as litter and to be relatively high below communities such as carr. It is not yet evident to what an extent such an effect is present in the fen.

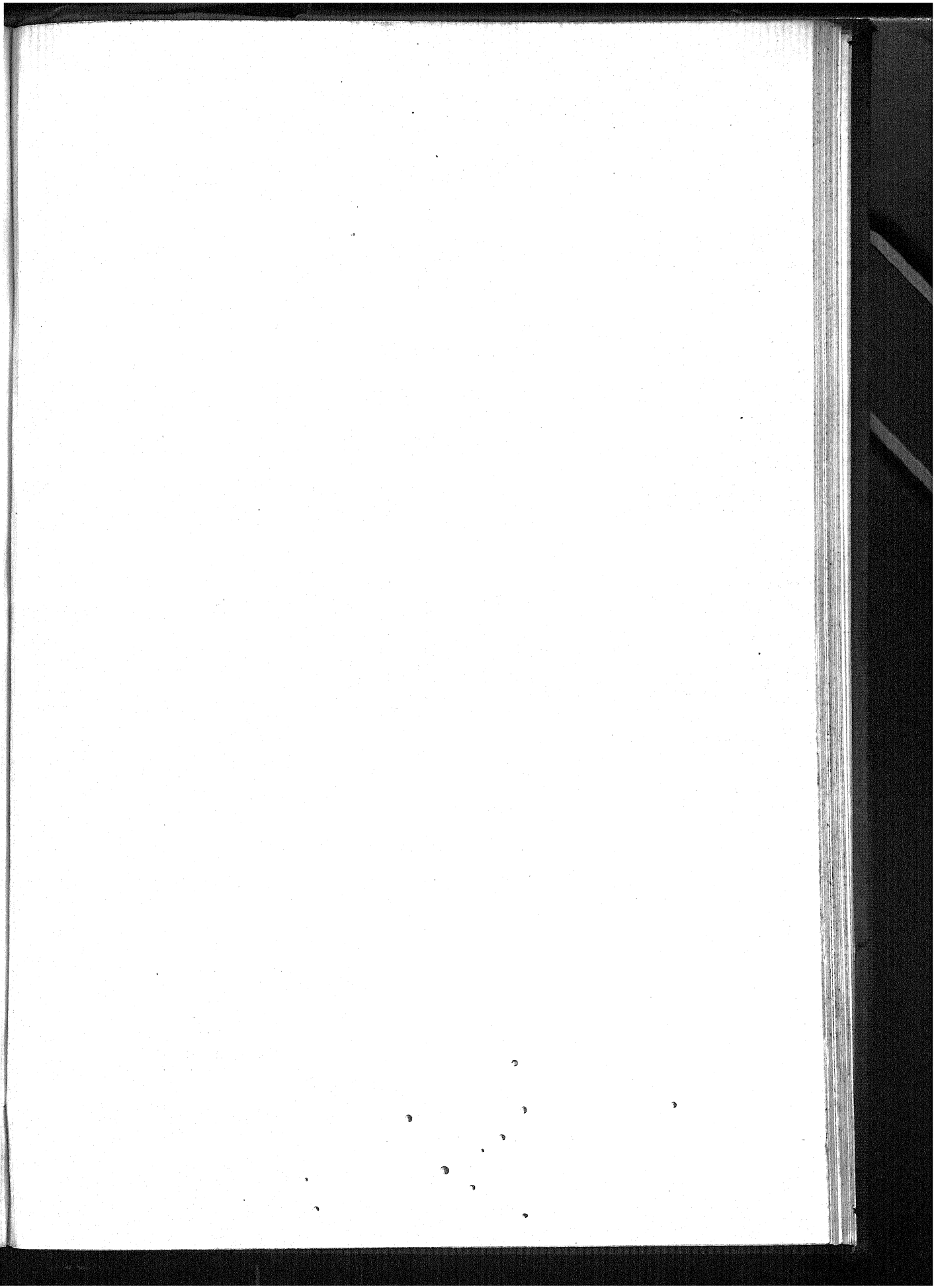
Variation in the water table produced in this way may possibly exercise control over distribution of plants on the fen but, as will be later suggested, it seems at present more likely that control takes place in the winter when the transpiration effect is negligible and the water table is more nearly flat all over the fen.

#### SUMMARY.

A description is given of an automatic water-level recording apparatus which has been set up in the fen for two-and-a-half years. The water-level records have been analysed in terms of the factors controlling the levels; these are the following:

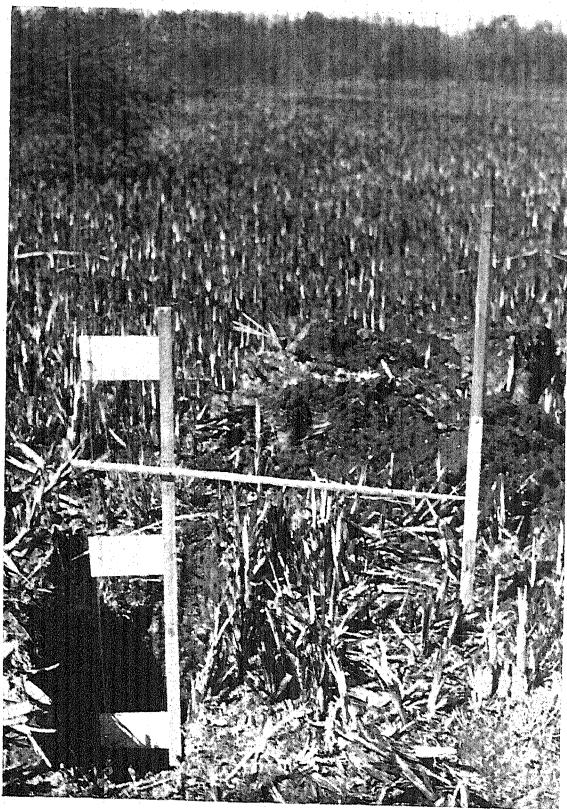
(1) *The fen drainage system*, which is in ultimate connection with sluice gates kept at a given level. This tends to prevent high water levels in winter, and to lessen the fall to low levels in summer. It narrows the range of movement of the water table as a whole.

(2) *The rainfall*, which is shown to be responsible for all the sudden rises in water level all over the fen. The rise in level is shown to agree roughly with the rainfall and soil pore-space data.

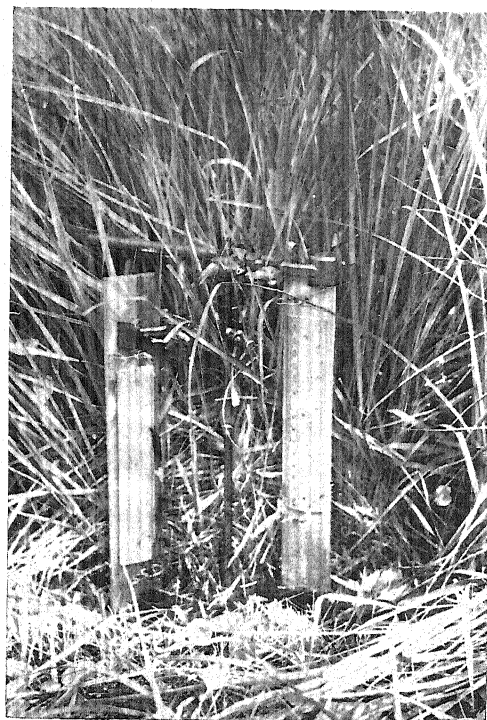




Phot. 1.



Phot. 2.



Phot. 3.

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Face p. 473



(3) *Transpiration*, which is shown to be effective in producing a fall in the fen water level each day during the months May to October. Close to the drainage channels the level recovers at night, but away from them the level is unaltered. In each there is a marked daily periodicity in level.

The foregoing factors are effective in producing a seasonal variation in level through the year, which can be divided into three periods:

A. November to June—high water table—phase of control by rainfall and locks of the drainage system.

B. June, July and August—phase of reduction of water level by heavy transpiration, and of maintained low levels.

C. September and October—phase of failure of transpiration and filling up of the fen by autumn rains—rising water levels.

Field measurements of change in water level were made with sensitive indicators and by two simultaneously recording instruments placed in different plant communities. These have shown that the magnitude of transpiration in litter vegetation is of the order of 3 to 4 litres per square metre per day in fine summer weather, whilst in mixed sedge recovering from fire the rate is about half, and in middle-aged carr less than half this amount. In ground bared of vegetation by fire the fall in water level each day is about one-fifth of that in the litter.

An "insert phytometer" apparatus is described, by means of which the water-level behaviour in an enclosed culture of fen vegetation can be compared with the behaviour of levels in the neighbouring fen. The results confirm the previous interpretations of the daily periodicity of water-level behaviour as phenomena of transpiration and drainage from lodes and dykes.

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- (1) Godwin, H. and Tansley, A. G. "The Vegetation of Wicken Fen." *The Natural History of Wicken Fen*, Part V, Cambridge, 1929.
- (2) Small, J. "Fenlands of Lough Neagh." *This JOURNAL*. 19, 2, p. 386.
- (3) Farren, W. S. "A note on the levels of the fens around Wicken." *The Natural History of Wicken Fen*, Part III, 1926.

#### EXPLANATION OF PLATE XXVII.

Phot. 1. The automatic water-level recorder set up at pit 17 in "litter" vegetation. The outer case is open showing the recorder. The pen arm is moved by a long lever arm fastened to the float in the pit behind.

Phot. 2. Sensitive level indicator set up in August 1929, 10 days after clearing up by fire. The spikes in the ground are the bases of *Cladium* with new white leaf-bases grown out since the fire.

Phot. 3. The insert phytometer experiment in July 1930. The clamps carry scales against which small paper indicators are visible. The indicators are carried on delicate glass rods running through guides and carried by floats in the two small wells, the necks of which can be seen below the scales. The vegetation consists largely of *Molinia caerulea* and *Carex panicea*.



# ECOLOGICAL INVESTIGATION IN SOUTH, CENTRAL AND EAST AFRICA: OUTLINE OF A PROGRESSIVE SCHEME

By JOHN PHILLIPS.

## I. INTRODUCTORY REMARKS.

In this brief communication I propose, without entering into particular details, to suggest the broad lines that I consider desirable for ecological investigations in South, Central and East Africa. The scheme is put forward entirely on my own responsibility, and not with the inspiration or authority of any government.

Ecological research being a relatively novel line in scientific investigation, it behoves us to be particularly careful that we base that research upon practical foundations that are sound, and upon concepts that are broad and dynamic. The points that appeal to me as being of the first importance are based upon my own experience in ecological research in South and East Africa.

The territory under consideration comprises that constituted by the Union of South Africa, Swaziland, Basutoland, Bechuanaland, Southern and Northern Rhodesia, Nyassaland, Uganda, Tanganyika and Kenya.

## II. OBJECTS OF AN ECOLOGICAL SURVEY IN SOUTH, CENTRAL AND EAST AFRICA.

For the sake of convenience the objects sought may be discussed under the somewhat unnatural divisions: *Scientific objects*, *Practical objects*—unnatural because the scientific objects fundamentally are related to the practical ones.

### (a) *Principal scientific objects.*

(1) To gain information as to the nature, development, and ecological interrelations of the more important *biotic* formations, and the succession stages leading to these.

(2) To obtain precise data as to the main *influent* habitat conditions within such *biotic* communities.

(3) To work out the indicator significance of these main *biotic* communities; to select the most effective factor, process, and practice indicators.

(4) To evolve the methods of ecological investigation best suited to the conditions holding in Africa.

It is to be noted that I use the term *biotic community* in place of the term *plant community*. I do this because my experience leads me to think that in Nature we deal with *biotic* communities only, and not with separate *plant* communities and separate *animal* communities.

This concept—due in the first place to Clements and Shelford—I have discussed in a paper read at the International Botanical Congress at Cambridge (This JOURN. 19).

(b) *Principal practical objects.*

To gather scientific information bearing directly and indirectly upon:

(1) The rational use of biotic communities in agricultural practice—so as to gain the best crops, and at the same time to conserve the soil characteristics, if not to improve them.

(2) The wise utilisation of natural grazing, the possible improvement thereof, the problems associated with herbage toxic to domesticated animals, and the nutritional values of pasturage.

(3) The development of progressive forest policies in the spheres of conservation, re-forestation, afforestation, silvicultural management, and forest protection.

(4) The prevention of soil erosion and its concomitant evils; and in certain local instances the reclamation of areas disturbed by accelerated erosion due to man's action.

(5) The conservation of moisture in natural water-catchment regions.

(6) The investigation and control of belts of tsetse fly, since these flies depend for their existence upon the vegetation types and the animals within such types.

III. SUGGESTED PROCEDURE.

(a) *The study of selected formations.*

A study of the available botanical information upon South and East Africa suggests that the main formations fall under the following general sub-heads: (i) desert; (ii) Karroo semi-desert scrub; (iii) Karroo semi-desert scrub-grass transition; (iv) climax grassland; (v) deciduous scrub (whose seral stages cover vast areas); (vi) subtropical evergreen scrub; (vii) Macchia or "Fijnbos" of the South-West Cape Province; (viii) subtropical evergreen forest; (ix) tropical evergreen forest; (x) mangrove swamp.

With the exception of the desert communities, these formations are of economic importance, either for agricultural and pastoral pursuits, or for the major and minor natural products yielded by them. Their investigation ecologically—as a basis for their most rational economic use—is therefore highly desirable. But the extent of territory with which we are concerned is so huge that normally the financial cost of investigating the principal formations within each separate governmental domain would be prohibitive. For this reason it is necessary that we should decide upon the particular formations it is most desirable to investigate. Thereafter we could work upon these within selected governmental territories only. If and when resources permit the study of the remaining formations within any single territory could be undertaken.

In order to decide how and where we are to study the selected formations the distribution of the main formations in the regions under discussion is briefly reviewed in the following table:

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Formations	Represented widely in	Represented to an important extent in
<b>I. DESERT</b>	Namib of South-West African coast belt	—
<b>SALT DESERT</b>	—	South-West Africa; Bechuanaland; Tanganyika
<b>II. KARROO SEMI-DESERT SHRUB CLIMAX</b>	Cape Province	Contiguous with Namib of South-West Africa
<b>III. KARROO SEMI-DESERT SHRUB-GRASS TRANSITION</b>	Contiguous with upper and lower Karroo of Cape Province, Namaqualand, and South-West Africa	Kenya (coast hinterland: 2° N. to 2° S. lat.)
<b>IV. CLIMAX GRASSLAND</b>		
(1) <i>SUBTROPICAL BUNCH-GRASS</i>	South Africa; Basutoland	Southern Rhodesia
(2) <i>TROPICAL HIGH GRASS</i> (possibly seral?)	Uganda	Sporadically in other Central and East African territories
(3) <i>MOUNTAIN GRASSLAND</i>	Tanganyika; Uganda	Kenya; Nyassaland
(4) <i>ALPINE MEADOW</i>	—	The uppermost portions of the higher mountains in Central and East Africa
(5) <i>MARSH GRASS</i> (possibly seral?)	—	Bechuanaland; Northern Rhodesia; Uganda
<b>V. DECIDUOUS SCRUB</b> (with its main seral stages covering great areas):	Bechuanaland; Northern and Southern Rhodesia; Tanganyika; Kenya	Nyassaland
(i) Seral grassland		
(ii) <i>Acacia</i> open woodland, with short or long grass		
(iii) Hydrophilous <i>Acacia</i> communities		
(iv) <i>Balanites</i> and palm communities		
(v) Hydrophilous fringing bush		
(vi) <i>Combretum-Terminalia</i> -other spp. open woodland		
(vii) <i>Berlinia</i> , <i>Brachystegia</i> , <i>Uapaca</i> , <i>Baikia</i> , <i>Copaifera</i> , etc. woodland		
The peculiar <i>Grewia-Pseudoprosopis-Bussea</i> thickets of the Singida-Manyoni type	—	Tanganyika
<b>VI. EVERGREEN SUB-TROPICAL SCRUB</b>	South Africa, especially the Cape Province	About 5000-6000 ft. in Central and East Africa
<b>VII. MACCHIA</b> or " <b>FIJNBOS</b> "	South-West Cape Province (seral in the Knysna region)	—
<b>VIII. SUBTROPICAL EVERGREEN FOREST</b> of various types, ranging from the <i>Podocarpus-Olea</i> -other spp. forests of the Knysna type to the rather more tropical forests of East Africa, and including the East African <i>Juniperus</i> and <i>Widdringtonia</i> types	—	South Africa (moister coast and montane regions); Southern Rhodesia, Northern Rhodesia, Nyassaland, Kenya, Uganda (highlands above 5000-7000 ft.)
<b>IX. TROPICAL EVERGREEN FOREST</b>	—	Nyassaland, Kenya (riverine), Uganda (scattered), Tanganyika (coast, lower slopes of coast-hinterland ranges, and Kilimanjaro)
(i) Coastal type		
(ii) Lower level (1600-4000 ft.) moister type		
(iii) Upper tropical "rain" forest type		
(iv) Lower level drier type		
<b>X. MANGROVE SWAMP</b>	—	Along the coasts of Zululand, Tanganyika, Kenya

*(b) Training of staff.*

One of the main difficulties is the obtaining of men with adequate training in, and with a particular *flair* for ecological research. This difficulty is, I venture to think, partly due to the fact that most of our Home and Overseas Universities take relatively little interest in the teaching of dynamic ecology. Our need as an Empire is great and urgent: could not our Universities endeavour to meet it?

On the grounds of my own shortcomings I should say that for the kind of ecological work urgently required in our overseas possessions, the best equipped ecologist is he who is qualified more or less as follows:

(1) The usual foundation of physical and biological science, with advanced study in both zoology and botany (a sound grounding in the systematic botany of the flowering plants is essential); and if possible also in either chemistry or physics.

(2) Thereafter a course in either agriculture or forestry, with the object of giving a theoretical and practical understanding of these important subjects.

(3) A special theoretical and practical course in field surveying and simple agricultural or forest engineering.

(4) A short course in statistics, almost certainly useful in the working out of biological data.

(5) Theoretical and practical training in geology, agricultural or forest chemistry, climatology, agricultural bacteriology, mycology, entomology, and selected methods of analysis of biotic communities and habitats.

(6) Experience in dealing with scientific literature, including a good working knowledge of the principal ecological literature.

(7) Practical training in photography and photographic methods.

(8) Practical experience in the efficient making, filing, and indexing of scientific and other records, and in simple general office methods. Only too often do we find university men entirely incapable of making and arranging adequate records or of doing simple accounts.

Such a training would require from five to six years of university life, but such periods are now commonly demanded of forest and agricultural officers.

For somewhat specialised ecological researches—as for example the problems set by the tsetse fly—a partial course in veterinary or medical science would be a definitely useful adjunct to the training already outlined.

I emphasise the need of giving ecologists training in such subjects as agriculture, forestry, veterinary or medical science, for the very good reason that without one or other of these (or in special instances all) ecologists cannot be expected to realise and understand the great practical problems set them in the field, nor can they hope to work in the fullest and most intelligent co-operation with officers engaged in these particular professions.

Even after the student has undergone the broad training described, he

cannot—except in outstanding instances—be considered capable of conducting ecological research in Africa or any other new country, unguided by an investigator of some experience. The newly qualified man, in my opinion, should serve for at least a year with such a senior in the particular overseas territory in which he is to work. During this period he would not only have an opportunity of learning how to proceed in practical investigations, but would also be able to build up a working knowledge of the systematic botany and zoology of the region. I suggest that this initial training of the staff in the field, by a senior, be considered an essential, at any rate so far as ecological investigations in South, Central and East Africa are concerned.

(c) *Distribution of staff.*

To attain the objects described the following personnel would be required:

(i) Seven senior research officers, twelve junior research officers, one secretary, fourteen lay assistants (European), together with several European (South Africa) and Asiatic (Central and East Africa) clerks. In charge of the whole there would be a director, whose whole duty should be to define the policy and concepts, guide the research officers, and generally co-ordinate the results of the investigations.

(ii) After the staff had obtained about a year's practical experience under the director's guidance, they might be distributed in some such manner as is shown in the following table:

Territory	Formations to be studied	Details re staff
Union of South Africa	(i) Karroo semi-desert shrub, and (ii) Karroid semi-desert shrub-grass transition	1 senior officer 1 junior officer 1 lay assistant
Union of South Africa	Grassland climax (subtropical bunch grass in Orange Free State and Transvaal)	1 senior officer 1 junior officer 1 lay assistant
Southern Rhodesia	Subtropical bunch grass, and seral tree-and-grass savanna	1 senior officer 1 lay assistant
Uganda, Uganda and Tanganyika	(i) Tropical high grass savanna, (ii) mountain grassland	1 senior officer 1 junior officer 1 lay assistant
Union of South Africa	Subtropical evergreen scrub of the Cape Province	1 junior officer 1 lay assistant —working under general guidance of senior officer studying the Karroo
Bechuanaland, Southern and Northern Rhodesia, Nyassaland, Tanganyika, Kenya	Deciduous scrub climax, with its main seral communities: (i) <i>Acacia</i> open woodland of various types; (ii) <i>Combretum</i> open woodland of various types; (iii) woodland of <i>Berlinia</i> , <i>Brachystegia</i> , <i>Baikia</i> , <i>Copaifera</i> , etc.	2 senior officers 5 junior officers 6 lay assistants
Union of South Africa	Macchia or "Fijnbos"	1 junior officer 1 lay assistant —collaborating with officers of the Botanical Survey and the Universities at the Cape



Territory	Formations to be studied	Details <i>re</i> staff
Nyassaland, Tanganyika, Kenya, Uganda	Subtropical evergreen forest, tropical evergreen forest	1 senior officer 2 junior officers 2 lay assistants —to collaborate with forest officers in these colonies; a beginning has been made by the Forest Department in South Africa (at Knysna)

The selection of a training centre for the staff would require careful thought, but at the present time it seems that a year spent in studying some of the main ecological features in the great areas of South and East Africa covered by the various seral stages of the deciduous scrub formation would be desirable. Not only would the staff receive training, but in addition would be contributing data toward the solution of problems of the first importance.

Following the training in this formation, the staff should be distributed among the formations to be studied. It is clear that much useful assistance could be obtained by the co-operation of the following government and other officers: *In South Africa*: Officers of the Bureau of Plant Industry, and the Botanical Survey; Forest, Agricultural College, and University officers. *In Rhodesia*: Agricultural and Forest officers. *In Central and East Africa*: Research officers of the Agricultural Research Station at Amani, Agricultural and Forest officers. It is conceivable that the Imperial College of Agriculture, Trinidad, might agree to sending several students each year, for the sake of learning ecological research methods in the field, and temporarily assisting the staff. Workers in official herbaria in Great Britain and South Africa would probably gladly co-operate in the naming of herbarium material, while animal collections would doubtless be identified by workers in museums and government institutions in Great Britain and South Africa.

Semi-permanent native assistants could be trained to aid in routine work and to supervise labour.

(d) *Outline of the research programme.*

It is necessary that such fundamental matters as the nomenclature and classification of communities, methods of community and habitat analysis, and the recording and working out of scientific data should be placed upon a uniform basis *ab initio*. Without such an arrangement the smooth running of the investigation and the attainment of the best scientific results could not be expected. In addition to these essential preliminaries, the general lines of procedure should include the following:

- (1) Settlement of administrative and financial details, and careful selection of the staff and equipment.
- (2) General reconnaissance by the Director and a senior officer through the territories to be studied.
- (3) Initial training of the staff in Africa, upon practical problems in, say,



the deciduous scrub formation; this training to include a working knowledge of the systematics of the plants and animals.

(4) Selection of the best working localities within the chosen formations in the various territories, selection of the most suitable officers for the particular work planned; arrangement for co-operation between ecologists and territorial administrative and scientific officers.

(5) Drawing up by officers in collaboration with the Director and any other scientific officers within the territory, of a programme of research most urgently required to be pursued within the particular territory.

(6) Local research programmes should, *inter alia*; take into account the following:

(a) Extensive systematic reconnaissance within and around the formation under study; instrumental observations of all necessary climatic, soil, and physiographic features; observations on vegetation communities and their animal associates, including the apparent successions. This reconnaissance would be primarily to suggest sites for, and lines of, research. It must, however, be continued from time to time throughout the period of investigation.

(b) Extensive and intensive successional studies within the biotic communities. The establishment of permanent quadrats and transects should be undertaken, so that they could be kept under observation by succeeding generations.

(c) Habitat analysis by the most efficient methods.

(d) Study of community reactions and interrelations—or the “co-actions” between plant and plant, plant and animal, animal and animal.

(e) Conduct of such special field experiments as might be found necessary for throwing light on particular aspects of certain ecological problems. Included here would be animal exclosure, fire protection, and cultural experiments.

(f) Working out intensively and extensively the indicator significance of the more widespread biotic communities, and applying the information so obtained to agriculture, pasturage management, or forestry—as circumstances indicated.

(g) In certain cases—such as the dominants of extensive and important communities—study of the principal biological and autecological features of selected species of plants and animals.

(h) Making, and submission to scientific authorities, of biological collections—emphasis being placed not upon rare or unique specimens, but upon organisms that appear to play some important rôle in the ecology of the formation.

(i) Keeping in touch with the broader needs of agriculture, officers concerned with pasture management, veterinary work and forestry, and applying the available scientific data wherever possible to practical ends. It is conceivable that from time to time this could be accomplished by means of large-scale, practical, but properly checked experiments.

(j) Gradually, by means of simple survey methods (e.g. compass traverses) the broad and fundamental ecological features of the region should be mapped; possibly aerial survey might be a useful adjunct.

(7) Co-ordination of the data returned by the officers studying the various formations.

(8) Preparation and publication of annual and periodic reports as well as special scientific papers.

#### IV. FINANCIAL OUTLAY: AN ESTIMATE.

On the basis of fairly detailed consideration of the necessary expenditure involved in the scheme outlined above, it is estimated that the *annual cost* of the scheme would amount to about £20,000 in stipends, salaries and wages, rising at the end of six to eight years to £25,000; and about £11,000 in other costs, such as equipment, travelling and incidental expenses, making a total of £31,000, rising to £36,000. In addition about £14,000 would be required as initial, non-recurrent expenditure on equipment and passages to Africa. It is proposed that the stipend of the Director should be £1500, of the senior research officers £600 to £800, rising to £750 or £1000 according to location, and of the junior research officers £400 or £600, rising to £750 or £800.

This outlay could—it is suggested—be shared by South Africa, Southern Rhodesia, Northern Rhodesia, Nyassaland, Uganda, Tanganyika, Kenya and the Protectorates of Bechuanaland, Swaziland and Basutoland, according to arrangements entered into by the authorities administering these territories.

#### V. ADMINISTRATIVE ARRANGEMENTS.

Owing to so many territories being concerned with an ecological survey of the type herein proposed, special care to base the investigation upon sound administrative principles would have to be exercised. In general it would seem to the advantage of the survey to place it upon the same footing as the East African Agricultural Research Station, Amani, Tanganyika—probably with some special arrangements for the officers serving in the Union of South Africa and in Southern Rhodesia. The Director should be responsible either to the Imperial Government, or to a special Ecological Survey Committee appointed by the Imperial, Territorial, South African and Southern Rhodesian Governments. The senior research officers in each territory or formation would be responsible to the Director.

Arrangements would have to be made with each Government concerned as regards buildings for official and residential purposes. The usual medical and other facilities available to government officials in the various territories should apply to the officers of the survey.

## VI. CONCLUSION.

Details of varying degrees of importance have been omitted, and these would require careful thought before the survey could be commenced. Ambitious as the general scheme may appear, costly as it certainly would be, there seems little reason why a modest beginning at least should not be attempted. Were this to be no more than a decision to proceed with the survey when funds and workers are available, together with an endeavour to give students a broader and deeper training in ecology, a definite step forward would have been taken. In South, Central and East Africa we have great possessions presenting wonderful scientific and economic opportunities—and it is incumbent upon us to develop them for the general advancement of civilisation. The necessary basis is a dynamic ecological survey in which the spirit of co-operative team work is one of the inspiring forces.

## NOTICES OF PUBLICATIONS ON ANIMAL ECOLOGY

By CHARLES ELTON.

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*Note.* The objects and scope of this system of abstracts are explained in This JOURN. **16**, p. 172 and p. 399, 1929.

### 1. GENERAL PAPERS ON PARTICULAR GROUPS OF ANIMALS.

**Laidlaw, W. B. R.** "The Pine-cone Weevil (*Pissodes validirostris*) in Britain; with a brief Comparative Account of the Genus *Pissodes*." *Scottish Nat.* pp. 79-84. 1931.

**Womersley, H.** "The Collembola of Ireland." *Proc. Royal Irish Acad.* Section B, **39**, pp. 160-202. 1930.

An important paper, containing keys to all the genera and species, together with a number of general notes on habitats.

**Lowndes, A. G.** "Some Rare and Little-known British Fresh-water Ostracods." *Rept. Marlborough College Nat. Hist. Soc.* **79**, pp. 82-112. 1930.

Descriptions and records of species already known from the Continent, here recorded for England. A number of diagrams and some photographs.

**Phillips, R. A. and Watson, H.** "*Milax gracilis* (Leydig) in the British Isles." *Journ. Conchology*, **19**, pp. 65-93. 1930.

A full description of the structure, habitat and habits of this slug both in Britain and Ireland, together with a table classifying the Limacidae, and coloured plates of *Milax gracilis*, *M. sowerbii*, and *M. gagates* var. *plumbeus*.

### 2. ECOLOGICAL SURVEYS AND HABITAT NOTES.

#### (a) MARINE.

See also Section 6 (Ellis, Steven).

**Wynne-Edwards, V. C.** "Birds of the North Atlantic." *Discovery*, **11**, No. 131. 1930.

A transect from England to Canada, showing the various zones of bird life which are similar on each side of the Atlantic.

**Russell, E. S.** "The Vertical Distribution of Marine Macroplankton: 9. The Distribution of the Pelagic Young of Teleostean Fishes in the Day-time in the Plymouth Area." *Journ. Marine Biol. Ass.* **16**, pp. 639-676. 1930.

The various species have different levels of maximum abundance. These vary, however, with weather (e.g. probably higher in some species on dull days), time of day (some species tend to come higher at night), local abundance of plankton, and proximity to the coast. There is evidence that young of summer-spawning species tend to occur higher than the young of spring-spawning species.

**Russell, E. S.** "The Seasonal Abundance and Distribution of the Pelagic Young of Teleostean Fishes caught in the Ring-trawl in Offshore Waters in the Plymouth Area." *Journ. Marine Biol. Ass.* **16**, pp. 707-722. 1930.

**Lambert, F. J.** "Animal Life in the Marsh Ditches of the Thames Estuary." *Proc. Zool. Soc. London*, pp. 801-808. 1930.

An interesting general account of the changes which accompany consolidation of land in estuaries, with special reference to the flora and fauna of the marsh ditches, for which lists of inhabitants are given. There are also notes on some of the species, and on seasonal variation in habitat factors in the ditches.

**Orton, J. H. and Moore, H. B.** "Occurrence of *Protodrilus flavocapitatus* at Port Erin." *Nature*, pp. 780-781. 1931.

A discussion of the habitat factors controlling the rather restricted habitat of this Archiannelid.

**Massy, A. L.** "Mollusca (Pelecypoda, Scaphopoda, Gastropoda, Opisthobranchia) of the Irish Atlantic Slope, 50-1500 fathoms." *Proc. Royal Irish Acad. Section B*, **39**, pp. 232-342. 1930.

A list of species, giving for each its world distribution, vertical range, fossil records, and new stations. There is an index to genera.

**Moore, H. B. and Neill, R. G.** "An Instrument for Sampling Marine Muds." *Journ. Marine Biol. Ass.* **16**, pp. 589-594. 1930.

(b) FRESH-WATER.

See also Section 2 (c) (Lloyd Praeger).

**Balfour-Browne, F.** "The Aquatic Coleoptera of Caithness and Sutherland." *Scottish Nat.* pp. 171-188. 1930.

A detailed study of the distribution of certain species in the British Isles, and of their geographical variation, e.g. in the two species *Deronectes depressus* and *D. elegans*.

**Omer-Cooper, J.** "Some Notes on Dytiscidae collected in Northumberland and Durham in 1930." *Vasculum*, **17**, pp. 43-50. 1931.

Useful habitat notes for Dytiscid beetles living in peat moss, running water, and fresh-water marsh, ponds, and lakes, together with incidental notes on distribution, abundance and variation, in which references to other counties occur.

**Kevan, D. K.** "Report on the Molluscan Fauna of Duddingston Sanctuary (with Supplement)." *Scottish Nat.* pp. 15-22 and 55-58. 1931.

Lists of species from different areas, with a certain number of habitat notes.

**Brown, J. W.** "A Contribution towards a Knowledge of the Fresh-water Rhizopoda of the English Lake District." *Ann. and Mag. of Nat. Hist.* Ser. 10, **7**, pp. 114-133. 1931.

A large collection from many lakes and tarns, together with a short discussion of habitats and lists of species restricted to sediment in lakes and tarns, to sphagnum, and to drier moss. One gathering was from moss high up on Helvellyn.

## (c) LAND.

See also Section 1 (Phillips and Watson); Section 6 (Ellis).

**Lloyd Praeger, R.** ed. by. "Report on Recent Additions to the Irish Fauna and Flora (Terrestrial and Fresh water)." *Proc. Royal Irish Acad. Sci.* Section B, **39**, pp. 1-94. 1929.

A comprehensive summary of the work done up to date, with full references to literature, and additional lists of some groups, full lists of others. Little ecological data, but much of use for distribution study. A valuable list of Aphides by F. V. Theobald, containing full habitat and host-plant data. The tapeworm, *Dibothriocephalus latus*, is recorded rarely from human beings.

**Middleton, A. D.** "A Contribution to the Biology of the Common Shrew, *Sorex araneus* Linnaeus." *Proc. Zool. Soc. London*, pp. 133-143. 1931.

Contains notes on habitats, food, day and night activity, enemies, sex ratio, reproduction, and seasonal age distributions of the population.

**Hibbert-Ware, A.** "Bird Life near Gilwell Park, Sewardstone." *Essex Nat.* **23**, pp. 67-82. 1931.

The lists of birds are grouped ecologically under buildings, small ponds, open spaces, woodland (high beech, and oak-hornbeam).

**Omer-Cooper, J.** "Some Notes on Dytiscidae collected in Northumberland and Durham in 1930." *Vasculum*, **17**, pp. 43-50. 1931.

Useful habitat notes for Dytiscid beetles living in peat moss, running water, and fresh-water marsh, ponds, and lakes, together with incidental notes on distribution, abundance, and variation, in which references to other counties occur.

**Laidlaw, W. B. R.** "Notes on Some Humble Bees and Wasps in Scotland: 2. The Social Wasps." *Scottish Nat.* pp. 135-136. 1930.

Notes on localities, dates of activity, and foods.

**Laidlaw, W. B. R.** "Additional Notes on Humble Bees in Scotland." *Scottish Nat.* pp. 23-24. 1931.

Scattered notes on dates of activity and flowers visited.

**Fox Wilson, G.** "Insect Pests of Hardy *Rhododendrons*: with Notes on Some Uncommon Damage." *Gardener's Chronicle*, March 28th, pp. 244-245. 1931.

The damage referred to was done by a moth *Batodes angustiorana*, the weevils *Otiorynchus sulcatus* and *O. picipes*, and by the Hemipteran *Dialeurodes chittendeni*. There is also a summarised list of twenty-two known pests of hardy *Rhododendrons*, giving their natural host plants in Surrey and the symptoms of their attack on *Rhododendrons*.

**Cameron, A. E.** "Two Species of Anthomyid Diptera attacking Bracken and their Hymenopterous Parasites." *Scottish Nat.* pp. 137-141. 1930.

Bracken has been spreading on upland sheep pastures in recent years, and is also established as a pest in New Zealand. A summary of previous work on insects attacking bracken is given. The parasites of two are discussed: of *Chirosia crassiseta*, a leaf-curler, and of *C. parvicornis*, a stem-miner. The former has an Ichneumonid and two Pteromalids, the latter a Braconid and a Cynipid. Both species were found to be heavily parasitised.



**Bristowe, W. S.** "The Spiders of the Island of Grassholm, and some Additions to the Skomer Island List (South Wales)." *Proc. Zool. Soc. London*, pp. 111-113. 1930.

Habitats of the species are given.

**Bristowe, W. S.** "A Contribution to the Knowledge of the Spider Fauna of South-west Ireland and, in particular, the Islands off the Coast." *Proc. Zool. Soc. London*, pp. 17-29. 1930.

Contains lists from different areas, together with biological observations, e.g. on habitats, aeronautic species (in which *Erigone dentipalpis* and *E. atra* predominated), a list from sandhills, seaweed drift, and mud flats, etc.

**Aubertin, D.** "The Natural History and Variation of the Pointed Snail, *Cochlicella acuta* (Mull.)" *Proc. Zool. Soc.*, pp. 1027-1055. 1930.

This species is mainly maritime in its distribution in the British Isles, with several curious exceptions, at present unexplained. Thus it occurs inland in Ireland, and in one or two places in the south of England. Large collections were made in order to determine the nature of colony differences in certain characters of the shells. Ecological notes are given for each collection, and include lists of other molluscs associated, lists of species of plants, and the pH values of the soils. Other observations include high rate of infestation in some areas by a parasitic Dipteran. The variation in colonies is fully discussed, and the authors conclude that these are due to the isolated nature of the colonies. Melanism shows a more consistent geographical gradation.

### 3. ANIMAL BEHAVIOUR AND THE ACTION OF ENVIRONMENTAL FACTORS.

See Section 7 on Numbers of Animals.

**Stenhouse, J. H.** "Swift *versus* Starling and Sparrow." *Scottish Nat.* pp. 73-78. 1931.

In early spring sparrows and starlings often compete for nesting places on buildings. Later on, the swift appears and contests the positions of both. Further observations are needed on this phase of animal competition.

**Hart, T. J.** "Preliminary Notes on the Bionomics of the Amphipod, *Corophium volutator* Pallas." *Journ. Marine Biol. Ass.* 16, pp. 761-789. 1930.

This distribution has a local distribution on mud flats in estuarine areas. The present study was made mainly in Whitby harbour. As a result of careful analysis of different soils, and study of salinity, etc. it is concluded that nature of soil is the limiting factor for this species. The food (mainly vegetable detritus), feeding methods, associated species, are discussed. It is pointed out that an allied species, *C. bonelli*, appears to be limited in the Danish fjords by salinity and not by soil.

**Boycott, A. E.** "A Re-survey of the Fresh-water Mollusca of the Parish of Aldenham after Ten Years, with Special Reference to the Effect of Drought." *Trans. Hertfordshire Nat. Hist. Soc.* 19, pp. 1-25. 1930.

Complete surveys were made in 1915-16, 1921, and 1925-28. 1921 was a year of severe drought. The effect of the drought on ninety-eight selected ponds is discussed. The effects upon molluscs were only great where drought was complete. There are a number of very interesting notes on the rate of colonisation of waters by molluscs, on methods of collecting

them, and of spotting species of water plants at different seasons, and a discussion of the relative importance of evaporation and percolation in the drying of ponds, together with notes on the periodic variations in these factors.

**Clapham, P. A.** "Observations on the Tropisms of *Dorylaimus saprophilus* and *Rhabditis succaris*." *Journ. Helminthology*, 9, pp. 29-38. 1931.

**Atkins, W. R. G. and Poole, H. H.** "The Photo-chemical and Photo-electric Measurement of Submarine Illumination." *Journ. Marine Biol. Ass.* 16, pp. 509-518. 1930.

Discusses experiments to determine the different values shown by the uranyl oxalate and the photo-electric methods.

**Choucroun, N.** "On the Hypothesis of Mitogenetic Radiation." *Journ. Marine Biol. Ass.* 17, pp. 65-74. 1930.

By ingenious experiments the author demonstrated that normal growth of the larvae of sea urchins (*Paracentrotus lividus*) was interfered with by placing below them cultures of *Bacterium tumefaciens* separated by quartz glass. The lower part of the apparatus was enclosed in paraffin. Controls were kept, but no detailed figures are given. The author contends that the experiments eliminated any possible "rays," since he was able to prevent the effect by placing a hollow stopper filled with sea water instead of the normal glass one in the flask containing the larvae. Again no figures are given.

#### 4. PARASITES OF ANIMALS.

See also Section 2 (c) (Lloyd Praeger).

**Main, H.** "Further Notes on *Methoca ichneumonides* (Latr.)." *Essex Nat.* 23, pp. 63-67. 1931.

This is a parasite of the tiger beetle (*Cicindela campestris*).

**Sikes, E. K.** "*Bairamlia fuscipes* Waterston, a Chalcidoid Parasite on *Ceratomyxus Wickhami* Baker (Siphonaptera)." *Parasitology*, 22, pp. 361-369. 1930.

Laboratory observations on the development of this parasite of the American grey squirrel flea, which occurred in about 7 per cent. of the flea cocoons in a nest from Gerrard's Cross, Bucks. A first attempt to parasitise cocoons of the Indian flea *Xenopsylla astia* failed.

**Slater, H.** "Aphaniptera (Siphonaptera)." *Proc. Somersetshire Arch. and Nat. Hist. Soc.* for 1929, p. liii. 1930.

Records three specimens of the flea *Ischnopsylla elongatus* from the greater horseshoe bat (*Nyctalus noctua*); also *I. simplex* (supposed to be found only on Natterer's bat, *Myotis Nattereri*) from the greater horseshoe bat and the whiskered bat, *Myotis mystacinus*.

**Oldham, J. N.** "On the Infestation of Elm Bark-beetles (Scolytidae) by a Nematode *Parasitylenchus scolyti* n.sp." *Journ. Helminthology*, 8, pp. 239-248. 1930.

The recent spread of the elm disease caused by the fungus *Graphium ulmi* in England has been accompanied by an increase in certain bark beetles (probably both as cause and effect). These species, *Scolytus destructor* and *S. multistriatus*, were found in one area to be heavily infested with nematodes, which occurred in about 60 per cent. of specimens, and

which in nearly 40 per cent. of specimens had caused parasitic castration of both sexes of both species of beetle. There were also numbers of free-living nematode worms, *Cylindrogaster ulmi*, on the outside of the beetles, in this way effecting dispersal. It is suggested that nematodes may be an effective check on increase of the beetles, and therefore to some extent of the elm disease fungus.

**Oldham, J. N.** "On the Arthropod Intermediate Hosts of *Hymenolepis diminuta* (Rudolphi 1819)." *Journ. Helminthology*, **9**, pp. 21-28. 1931.

This tapeworm occurs in the intestine of rats and other rodents and rarely in man. A complete list of the twenty-three species of arthropod hosts is given (including Myriapoda, cockroaches, an earwig, moths, fleas, and beetles). The fleas of the American grey squirrel in England were successfully infected with the eggs of this tapeworm.

**Morgan, D. O.** "On the Occurrence of *Hepaticola hepatica* as a Natural Infection of the Wild Rabbit in England." *Journ. Helminthology*, **9**, pp. 39-40. 1931.

One rabbit found to have liver diseased with this worm. No locality or date given.

**Baylis, H. A.** "Gammarus as an Intermediate Host for Trout Parasites." *Ann. and Mag. of Nat. Hist.* Ser. 10, **7**, pp. 431-436. 1931.

One hundred Gammarus from the River Test were examined for the larva of the cestode *Cyathocephalus truncatus* which had been found in trout from the same river. No specimens of this parasite were found, but three other larval worms occurred: *Crepidostomum furionis*, *Cystidicola? furionis*, and *Distomum agamos*.

**Ray, H. N.** "Studies on Some Sporozoa in Polychaete Worms: 1. Gregarines of the Genus *Selenidium*." *Parasitology*, **22**, pp. 370-398. 1930.

Polychaete worms at Plymouth have abundant Protozoan (and especially Sporozoan fauna), e.g. *Scolecopsis fuliginosa* had seven Protozoan parasites (five Sporozoa, a Ciliate, and a Dinoflagellate).

#### 5. PLANT-GALLS.

**Hurst, C. P.** "Plant Galls." *Rept. Marlborough College Nat. Hist. Soc.* **79**, p. 124. 1930.

Dipterous species from *Salix purpurea* and *Polygonum viviparum*.

**Dallman, A. A.** "Galling of *Salix herbacea* L." *North Western Nat.* **5**, p. 185. 1930.

Abundant on *Salix* on Carnedd Dafydd in North Wales at 3000-3200 feet.

**Graham, R.** "Galling of *Salix herbacea* L. in Lakeland." *North Western Nat.* **5**, p. 249. 1930.

Record from the High Street range.

**Goodey, T.** "On *Tylenchus agrostis* (Steinbuch 1799)." *Journ. Helminthology*, **8**, pp. 199-210. 1930.

Study of specimens from galls on *Agrostis stolonifera*, one of several species of grass parasitised by this roundworm. Also a comparison with the allied species which occurs on wheat. The author's examination of the structure confirms experimental work showing that the two species are distinct.

## 6. FOOD-HABITS.

See also Section 7 (Middleton).

Ellis, A. E. "Mollusca on Gateholm." *Journ. Conchology*, 19, pp. 61-62. 1930.

Notes on occurrence and habitats of land and intertidal molluscs on this island, which is off Pembrokeshire. The vertical range of *Littorina rudis* on the shore is very great. Rats devour large numbers of molluscs on the island; mainly *Cepaea*, limpets, and mussels. Other species are also eaten, together with shore crabs, *Carcinus moenas*.

Ingram, G. C. S. "Redstarts Feeding upon Elderberries." *British Birds*, 24, p. 127. 1930.

Lewis, S. "Crossbills eating Apples." *British Birds*, 24, pp. 125-126. 1930.

An editorial note adds that there was a great invasion of certain French departments by crossbills in 1930, and that destruction was done by them in apple orchards. In early years the crossbill used to eat apples commonly in England, but has changed its feeding habits so that there are no such records since 1869. This may be connected with the great increase in conifers in this country, providing the normal crossbill diet. See also note in *British Birds*, 24, p. 189, on crossbill eating crab-apples in Ireland.

Steven, G. A. "Bottom Fauna and the Food of Fishes." *Journ. Marine Biol. Ass.* 16, pp. 677-700. 1930.

The bottom fauna of about thirteen square miles off Plymouth was investigated for one year by means of periodic hauls at fifteen stations using both the Petersen grab and the Agassiz trawl. These were correlated with stomach examinations of 2000 fish belonging to twenty-nine species from the same area. The results, and also the feeding habits of the fish are described in detail. It is pointed out that the continuous carnivorous feeding of many fish from an early age complicates their food relationships very much in comparison with land mammalian carnivores which are looked after by their parents during early life. Some evidence of seasonal migration in certain Crustacea on the bottom was noted.

Paterson, N. F. "Studies on the Chrysomelidae: Part 1. The Bionomics, and Morphology of the Early Stages of *Paraphaedon tumidulus* Germ (Coleoptera, Phytophaga, Chrysomelidae)." *Proc. Zool. Soc. London*, pp. 627-676. 1930.

The larvae feed gregariously on the leaves of *Anthriscus sylvestris*, *Heracleum sphondylium*, and *H. sativum*, sometimes causing considerable damage to the plants. There are occasional records of injury to cultivated plants which show that the species is a potential pest. Experiments of transferring adults and larvae to pear, apple, mustard, and potato, resulted in refusal of the beetles to eat these plants.

Boycott, A. E. and Oldham, C. "On the feeding habits of *Geomalacus maculosus*." *Journ. Conchology*, 19, p. 36. 1930.

This species was studied in Cork, where it was living on rocks covered with lichens and mosses. In one place the slugs had been eating mainly *Parmelia perlata* and *Rhacomitrium*, in another area *Pertusaria areolata* and *Bacidia umbrina*. The authors conclude that food is varied and does not form a limiting factor to the distribution of this Lusitanian species.

## 7. THE NUMBERS ON ANIMALS.

See also Section 4 (Oldham).

**Middleton, A. D.** "The Ecology of the American Grey Squirrel (*Sciurus carolinensis* Gmelin) in the British Isles." *Proc. Zool. Soc. London*, pp. 809-843. 1930.

A comprehensive study of this introduced species, based on a large-scale enquiry from observers in different parts of the country, and on personal investigations. Thirty-three different centres of introduction are noted between the years 1889 and 1929. Over 13,000 square miles are already occupied. The study of inter-relations between red and grey squirrels is complicated by the existence of large natural fluctuations in the red squirrels, associated with outbreaks of disease. It is concluded that the grey squirrel may be a factor in preventing return of the red after periods of scarcity, but has not been responsible for its widespread decrease. A number of notes on food, enemies, breeding, habitats, etc., are included, together with four maps showing distribution at the time of writing.

**Munro, T. M.** "Musquash in Scotland." *Scottish Nat.* pp. 65-70. 1931.

Five individuals of this rodent were introduced from Canada into Central Europe in 1905. It is now ranked as one of the major pests of that region. In one year, about 1926, 33,000 were killed in Bavaria alone, and the present muskrat population of Central Europe is estimated at somewhere about a hundred million. The muskrat causes very serious and costly damage by burrowing into dams and banks of reservoirs, canals, etc. In 1927 it was introduced by fur farmers into Scotland. About ten animals escaped in that year. The muskrat is now firmly established wild in three areas, and appears to be flourishing.

**Harrison, T. H. and Hollom, P. A. D.** "Great Crested Grebe Inquiry (1931)." *Scottish Nat.* pp. 41-43. 1931.

An appeal for help in Scotland for the extensive investigation which is being sponsored by *British Birds*. The object is to carry out a census of the grebe populations in different parts of Great Britain, with special relation to their ecology and the reasons for their recent increase in numbers and range. Observers are asked to communicate with T. H. Harrison, Pembroke College, Cambridge.

**Blathwayt, F. L. and Tucker, B. W.** "Report on Somerset Birds, 1928." *15th Report of Ornithological Section of Somersetshire Arch. and Nat. Hist. Soc.* 1929.

Contains numerous notes, impossible to summarise, concerned with occurrence, migration, breeding, etc. The following seven species were selected for more special observations on numbers, etc.: siskin, mistle thrush, sand martin, tawny owl, barn owl, long-eared owl, short-eared owl, little owl, and lapwing.

**Blathwayt, F. L. and Tucker, B. W.** "Report on Somerset Birds, 1929." *16th Report of Ornithological Section of Somersetshire Arch. and Nat. Hist. Soc.* 1930.

Continuation of observations of the type mentioned in the last abstract, together with special observation on distribution and numbers, etc., of a number of ducks, and of goosander, merganser, and spew.



**Tucker, B. W.** "The Heron (*Ardea cinerea*) in Somerset: Part 1. The Breeding Places of the Heron in Somerset." *Proc. Somersetshire Arch. and Nat. Hist. Soc.* for 1929, pp. 61-90. 1930.

An important and accurate account of the heronries, for each of which the number of nests in 1929 is given, together with all available previous records, and a great deal of valuable data concerning the circumstances of increase and decrease.

**M'Conachie, W.** "Reappearance of the Goldfinch in the Eastern Borders." *Scottish Nat.* pp. 3-6. 1931.

The goldfinch had decreased greatly at the end of the last century, probably owing to persecution by bird-catchers. It has been greatly increasing during recent years, since the introduction of the Wild Birds Protection Act. A further note is given on p. 40, 1931.

**Adkin, R.** "On the Occasional Extensions of Territory by the Brown-tailed Moth, *Nygmia phaeorrhoea*, and its Ultimate Collapse." *Proc. South London Ent. and Nat. Hist. Soc.* for 1929-30, pp. 7-11. 1930.

This species normally occurs in colonies in rather restricted areas, but occasionally during the last hundred years has greatly increased and spread in certain years. This increase is followed by sudden disappearance. The author believes this is due to outbreaks of disease, but no direct evidence was obtained.

**Fergusson, A.** "*Phyllodrepana crenata*, Grav., in East Inverness and East Perth." *Scottish Nat.* p. 36. 1931.

This bark beetle is spreading southwards and northwards.

#### 8. MIGRATION AND DISPERSAL.

See also Section 6 (Lewis).

**Witherby, H. F.** "Ospreys in Great Britain." *British Birds*, 24, pp. 163-165, and 192-193 (1930), and p. 221 (1931).

There was an unusual immigration in the autumn of 1930.

**Witherby, H. F.** "Immigration of Crossbills in 1930." *British Birds*, 24, pp. 155-156 (1930), and p. 220 (1931).

Also notes on crossbills breeding in Surrey, *British Birds*, p. 156, 1930.

**Forrest, H. E.** "Crossbills in Shropshire." *North Western Nat.* 5, pp. 247-248, 1930.

**Reid, T.** "Crossbills at Selkirk." *Scottish Nat.* p. 134, 1930.

Further notes by other observers of crossbills in Scotland are given on pp. 134 and 170, 1930, and pp. 26, 46, 1931.

**Fox Wilson, G.** "Insects associated with the Seeds of Garden Plants." *Contr. from the Wisley Laboratory: J. Royal Hortic. Soc.* 66, pp. 31-47. 1931.

Description of pests which may be carried in seeds or associated with them, together with much ecological data, and notes on possible control measures.



Daltry, H. W. "Entomology." *Trans. and Ann. Rept. North Staffords. Field Club*, 63, p. 124. 1929.

1928 was a great year of butterfly and moth immigration from the Continent. A number of notes on different species.

Anon (Editorial). "The Convolvulus Hawk-moth in Scotland." *Scottish Nat.* pp. 129-132. 1930.

A summary of notes received from a number of observers on the appearance of this Continental migrant in Scotland in 1930. Further notes given on pp. 24 and 64, 1931. Similar notes from Ireland are given in *Irish Nat. Journ.* 3, pp. 133 (1930), and pp. 156-157 (1931).

Palmer, R. "Dragonflies observed in Hertfordshire." *Trans. Hertfordshire Nat. Hist. Soc.* 19, pp. 48-50. 1930.

Contains mainly records of occurrence in different localities. *Sympetrum flaveolum*, which is an immigrant from the Continent in certain years, was seen in 1926 in Hertfordshire, and also in other parts of the country.

Berrill, N. J. "On the Occurrence and Habits of the Siphonophore *Stephano-mia bijuga* (Delle Chiaje)." *Journ. Marine Biol. Ass.* 16, pp. 753-755. 1930.

Records the appearance of this species (very rare in the English Channel) in large numbers in Salcombe Estuary in May, 1929. Its habits were watched in the aquarium.

Supplement VII

BRITISH EMPIRE VEGETATION ABSTRACTS:

TITLES AND ABSTRACTS OF PUBLICATIONS ON THE  
VEGETATION AND ECOLOGY OF THE OVERSEAS  
EMPIRE AND ON RELATED TOPICS

(1) CANADA (COLLABORATOR, J. E. DANDY)

369. Louis-Marie, Father. "The Genus *Trisetum* in America." *Rhodora*, 30, pp. 209-223, 237-245. 1928-29. (1. 102.)

This is a brief account of a more comprehensive work which the author intends to publish as a Contribution from the Dept. of Botany of the University of Montreal. An analytical key to the subgenera, sections, and subsections is provided, followed by an enumeration of the species in their groups. New species, varieties, and forms are described, and many new names and combinations are proposed.

370. Setchell, W. A. "Morphological and Phenological Notes on *Zostera marina* L." *Univ. Calif. Publ. Bot.* 14, pp. 389-452, Figs. 1-59. 1929. (1. 103.)

In this paper the author gives a well-illustrated account of the taxonomy, morphology and development, and phenology of *Zostera marina*. The species is distributed along the Atlantic coast of North America from western Greenland to Beaufort, North Carolina; and along the Pacific coast, chiefly in the form of var. *latifolia*, from Unalaska Bay to San Diego, California, with some indication of extension to Guadalupe Island and Magdalena Bay in Mexico. A survey of the distribution and phenology of the species on the coasts of Europe from the Mediterranean to the White Sea shows early reproductive season in the south, becoming later and later in the localities north, a similar condition to that noted in the behaviour along the Atlantic coast of North America. The main variations within the species are vars. *angustifolia*, *typica*, *stenophylla*, and *latifolia*. Of these the first is not discussed, for lack of experience. The second and third may be edaphic variants, while the fourth may possibly be an ecad in the reversible sense of Clements, or possibly a fixed ecotype in the sense of Turesson.

371. Watson, E. E. "Contributions to a Monograph of the Genus *Helianthus*." *Pap. Michigan Acad. Sci.* 9, pp. 305-476, Plates 47-86. 1929. (1. 104.)

A systematic account of the genus *Helianthus*, with an artificial key to the species and a detailed enumeration of them. The number of species recognised is 108, of which several occur in Canada as wild or naturalised plants.

372. Smith, H. I. "Materia Medica of the Bella Coola and Neighbouring Tribes of British Columbia." *Nation. Mus. Can. Bull.* 56, pp. 47-68. 1929. (1. 105.)

This article describes the materia medica of four tribes of British Columbia, namely the Bella Coola of Bella Coola valley, the Gitksan of Skeena River, the Carrier who live in the territory behind both of these tribes, and the Sikani of the headwaters of Peace River.

373. Mousley, H. "Notes on the Birds, Orchids, Ferns and Butterflies of the Province of Quebec, 1928." *Can. Field-Naturalist*, **43**, pp. 93-99. 1929. (1. 106.)

374. Groh, H. "Gumweed (*Grindelia squarrosa* (Pursh) Dunal) in Ontario." *Can. Field-Naturalist*, **43**, pp. 106-107. 1929. (1. 107.)

A short account of the occurrence and history of *Grindelia squarrosa* in eastern Canada. No records whatever are at hand from any point east of the neighbourhood of Ottawa, Ontario. The species appears to have been first recorded in Ontario in 1891, from a locality near Ottawa. It has now been found in at least twenty-two counties throughout Old Ontario, and westwards to the Manitoba boundary where it begins to be indigenous. See Abstract 313.

Another western Composite, *Madia glomerata*, is recorded from Trois Pistoles, Temiscouata Co., Quebec, where it was said to be growing in a hay-field and was regarded as being weedy and established.

375. Groh, H. "Western Ragweed Farther East." *Can. Field-Naturalist*, **43**, p. 137. 1929. (1. 108.)

The author records *Ambrosia psilostachya* from rubbish-heaps at Harrington Harbour, Saguenay Co., Quebec, which may safely be regarded as the easternmost record for the continent. A small colony was also noted growing near farm-buildings at South Berwick, Nova Scotia. See Abstract 219.

376. Fairbairn, H. W. "The Distribution of the Basswood at Parry Sound, Ontario." *Can. Field-Naturalist*, **43**, pp. 188-189. 1929. (1. 109.)

During geological work near Parry Sound a field-relation involving *Tilia americana* (basswood) and crystalline limestone was discovered. Both the basswood and the limestone are sufficiently uncommon in the district to be worthy of note, and it was noticed that basswoods were commonly present near the limestone formations. Close scrutiny showed that in no case was a basswood found at any distance from an outcrop of limestone. Practical use of this relationship was made in tracing limestone formations in burned-over country, the basswood growing in small clumps and being easily separated at a distance, through its conspicuous foliage, from the other second-growth trees.

377. Marie-Victorin, Frère. "Le Dynamisme dans la Flore du Québec." *Contrib. Lab. Bot. Univ. Montréal*, **13**, pp. 1-89, Figs. 1-42. 1929. (1. 110.)

A survey (in French) of the flora of Quebec as influenced by the dynamic forces which have affected and are affecting it. The forces considered are firstly the intrinsic influences, including the forces of evolution and of elimination; and secondly the extrinsic influences, which are due particularly to the intelligent activity of man.

378. Marie-Victorin, Frère. "Les Liliiflores du Québec." *Contrib. Lab. Bot. Univ. Montréal*, **14**, pp. 1-202, Figs. 1-75. 1929. (1. 111.)

A systematic account (in French) of the Liliiflorae of Quebec, the families represented being the Liliaceae, Pontederiaceae, Iridaceae, and Juncaceae. Analytical keys are provided to the families, genera, and species, and often also to the varieties and forms. One variety (*Smilacina stellata* var. *crassa*) and a number of forms are described as new, and new combinations are proposed for several others.

379. Marie-Victorin, Frère. "Additions aux Cyperacées de l'Amérique du Nord." *Trans. Roy. Soc. Can. Ser. III*, **23**, Sect. v, pp. 253-268, Figs. 1-8, Plates 1-2 (*Contrib. Lab. Bot. Univ. Montréal*, **15**, pp. 253-268, Figs. 1-8, Plates 1-2). 1929. (1. 112.)

*Scirpus alpinus* is reported from the Mingan Archipelago and from Anticosti Island. *Carex vesicaria* var. *Grahamii* is recorded from Anticosti Island; this is an addition to the American flora. A new variety, *C. Oederi* var. *Rousseauiana*, is described from Quebec; it is an estuarine phase of *C. Oederi*, and is one of the plants which characterise the fresh-water tidal shores of the St Lawrence. *C. disticha* and *C. nutans*, two Old World species, are reported as established together in the Boucherville Islands, in the St Lawrence near Montreal. A new viviparous form, *Scirpus atrovirens* var. *georgianus* f. *viviparus*, is described from localities in the vicinity of Montreal. The paper is in French.

380. Hutchinson, A. H., Lucas, C. C., and McPhail, M. "Seasonal Variations in the Chemical and Physical Properties of the Waters of the Strait of Georgia in Relation to Phytoplankton." *Trans. Roy. Soc. Can. Ser. III*, **23**, Sect. v, pp. 177-187, Plates 1-2. 1929. (1. 113.)

This paper is an account of determinations of temperatures, salinities, pH, and phytoplankton extending over a period of nearly 3 years, and determinations of silica, phosphates, and oxygen during two summers and one winter, at a number of stations in the Strait of Georgia (British Columbia), particularly at the so-called Station 1, which is situated on a line between Nanaimo and Seechelt, approximately 10 miles from the former and 30 miles north-west of the Fraser River mouth. Records continued over 3 years demonstrate that there are seasonal fluctuations in the Strait of Georgia as follow:

- (1) A surface temperature change ranging from 1° C. to 22° C.; at 100 yards the seasonal variation is 3.5° C. only; at the surface a temperature above 17° C. is maintained over a considerable period of the summer. A stable epilimnion is formed in the summer, and vertical mixing takes place during the winter. The changes, both of decrease and increase in temperature, lag in time in proportion to the depth.
- (2) There is a marked lowering of the surface salinity even at a distance of 30 miles from the Fraser River mouth, the value of 8.5 gm. halide per l. being recorded for the summer; at the same place in the winter the value is 15.0 gm. per l. At greater depths the variation is proportionately less and the changes lag in point of time.
- (3) There is the greatest variation in pH at the surface; in winter 8.0 and in summer 8.8 approximates the limits of variability. High pH is associated with abundant phytoplankton and low salinity of the summer months, and the reverse is the case in the winter.
- (4) There are definite seasonal fluctuations in both the quantity of phytoplankton and the genera represented.
- (5) The phosphate and silicate values are much higher than obtain in the open sea. Diatoms decrease the amount of silica (but not to the point where they limit their own growth in these waters) since the greatest numbers of diatoms are associated with the lowest phosphate and silicate values. The Fraser River contributes silica and phosphates which are conserved within the basin of the Strait of Georgia.

381. Ormerod, M. J. and White, F. D. "A Preliminary Pharmacological Investigation of Extracts of Certain Western Canadian Plants." *Trans. Roy. Soc. Can. Ser. III*, **23**, Sect. v, pp. 189-194. 1929. (1. 114.)

Extracts of various western Canadian plants have been shown to possess definite pharmacological activity, *Caltha palustris*, *Cypripedium parviflorum*, *Rhus glabra*, and *Aralia*

*nudicaulis* being the most potent. In this investigation the plants studied were: *A. nudicaulis* (root), *Caltha palustris* (stem), *Cypripedium parviflorum* (stem), *Orchis rotundifolia* (leaves and stem combined), *Padus virginiana* (mesocarp), *Pulsatilla patens* (flowers and stem combined), and *R. glabra* (root).

382. Bisby, G. R., Buller, A. H. R., and Dearness, J. *The Fungi of Manitoba*, pp. i-xii + 1-194, Fig. 1. 1929. (1. 115.)

In this book an attempt has been made to give a complete census of the known fungi of Manitoba. Following a preface by E. J. Butler and a map showing the Floral Zones of Manitoba, the work is divided into nineteen sections, as follow: I. Introduction; II. The Natural Features of Manitoba; III. Geographical Distribution; IV. The Fungi of Particular Areas; V. Immigration and Ecology; VI. Coprophilous Fungi; VII. New Species (thirty-four new species and two new varieties are described in the book); VIII. Rare Species; IX. Fungi Apparently Absent; X. Estimates of the Total Number of Species of Fungi in Manitoba; XI. Statistical Summary; XII. History of Observations on the Fungi of Manitoba; XIII. The Groups of Fungi and Acknowledgments for Assistance in Determining Species; XIV. List of Species (including a separate list, by A. M. Davidson, of the fungi on man and higher animals observed at Winnipeg); XV. The Lichens of Manitoba (by Kirk Scott Wright); XVI. Index of Hosts or Substrata of Caulicolous and Lignicolous Fungi; XVII. Host Index of Parasitic Fungi; XVIII. Bibliography; XIX. Index of Classes, Orders, Families, and Genera.

383. Brown, Margaret S. "Bryophytes of Nova Scotia. Additional List." *The Bryologist*, 32, pp. 50-56. 1929. (1. 116.)

A list of 128 species of Bryophyta, collected—all but three—on the mainland of Nova Scotia. Of these species forty-two are new to the province; the remaining eighty-six have already been reported from Cape Breton Island, but not from the mainland. The additions bring the total number of species up to 449, i.e. 117 hepatics and 332 mosses.

384. MacFadden, F. A. "British Columbia the Bryologist's Paradise." *The Bryologist*, 32, pp. 56-61. 1929. (1. 117.)

An account of a tour in British Columbia, with special reference to some of the bryophytes encountered.

385. Dupret, H. "Three *Brachythecia* Hard to Separate from One Another." *The Bryologist*, 32, pp. 73-74, Fig. 1. 1929. (1. 118.)

An illustrated note on the differential characters of *Brachythecium rivulare*, *B. rutabulum*, and *B. Starkii*. These three mosses all occur in Canada.

386. Moxley, E. A. "Mosses of the Bruce Peninsula, Ontario." *The Bryologist*, 32, p. 84. 1929. (1. 119.)

This is an additional list to that published by the same author in *Can. Field-Naturalist*, 42, pp. 194-201 (1928). See Abstract 253.

387. MacFadden, F. A. "Easter Week at Halcyon Hot Springs, British Columbia." *The Bryologist*, 32, pp. 100-104. 1929. (1. 120.)

A description of expeditions made by the author during a week's stay at Halcyon Hot Springs, British Columbia, with a list of the species of mosses collected.



388. Dowding, Eleanör S. "The Vegetation of Alberta. III. The Sandhill Areas of Central Alberta with Particular Reference to the Ecology of *Arceuthobium americanum* Nutt." *Journ. of Ecology*, 17, pp. 82-105, Maps 1-2, Figs. 1-3, Plates 8-13. 1929. (1. 121.)

The large areas of sand-hills found in some regions of Alberta provoked interest by reason of the sharp contrast of their flora with that of the rest of the province. The tall pines on the summits of the sand-hills stood out in marked relief against the poplar-woods of the lower plain, and a closer investigation showed that the whole vegetation was quite distinct from that of the parkland. Moreover, the sand-hills themselves presented abrupt transitions from one association to another, such marked changes being chiefly due to differences in water-content and aspect. These sand-hills merited further attention because of the abundance of *Arceuthobium americanum* (Jack Pine Mistletoe), which was revealed by the strange deformities known as Witches' Brooms on the trees, giving them a weird tufted outline. The large amount of fresh material of the mistletoe available to the laboratories of the University of Alberta seemed to offer an exceptional opportunity for an investigation of the biology and ecology of this parasite. Further, the desire to give a comprehensive account of sand-hill vegetation naturally led to the investigation of wind-deposited as well as water-deposited sand-areas, although the former are outside the limit of distribution of *Pinus Banksiana* and hence of *A. americanum*.

For the investigation of the wind-deposited sand-areas an examination was made of the area of sand-dunes which is situated at the north-eastern end of Brule Lake. An investigation was carried out of the plants responsible for dune-formation and for dune-stabilisation. The effect of sand-deposition on the forests of the Brule valley was also observed.

Of the water-deposited sand-hills of Alberta the ones that were studied in greatest detail were those lying within a hundred-mile radius to the north of Edmonton. The different associations here arising in response to differences in water-content of the sand were recorded and described. These sand-hills were compared with those further west of which the vegetation showed further stages of development.

It was found that the mistletoe flourished to its greatest extent on the dry hill-summits, this being the result of its natural preference for a dry locality with maximum exposure to the sun. Also any spread to the more mesophytic associations was checked by the frequent fires on the flats and by the presence of a mistletoe-disease which flourished in the damper areas.

The spread of the *Arceuthobium* is surprisingly slow although its seeds may travel as far as 11 yards on being expelled. This may be explained by the natural resistance of the host.

In describing the effect of the parasite on the pine-branches it was noted, among other things, that the female plant has a more marked effect than the male, and also that infected pine-branches retain their leaves several years longer than is normal.

In examining numbers of trees no definite correlation was found between the degree of infection and the rate of growth of the wood except in cases of very severe infection.

The aerial part of the mistletoe in this locality is perennial, producing several crops of flowers. The flowers are pollinated in May, and the fruits so formed remain on the plant for two summers, exploding in September of the second summer. The seeds germinate on the pine-bark during June of the third summer.

389. Harshberger, J. W. "The Vegetation of the Screes, or Talus Slopes of Western North America." *Proc. Amer. Phil. Soc.* 68, pp. 13-25, Figs. 1-7. 1929. (1. 122.)

The author presents this paper as an introduction to the ecological investigation of American rock and scree plants. His account is based on the personal collections and observa-



tions made by himself in Glacier National Park (Montana), on the upper slopes of Mount Rainier (Washington), and on the Canadian Rocky Mountains. Supplementary observations are made on several plants collected on Alta Peak at 11,000 feet in the Sierra Nevada mountains of California. A list is given of the plants collected in these five regions, and this is followed by notes on the growth-forms of the scree plants of western North America, illustrated by photographs. The paper includes also a summary of European investigations on scree plants.

390. St John, H. "*Calluna vulgaris*, a Recent Adventive on Sable Island, Nova Scotia." *Journ. of Bot.* **67**, pp. 306-307. 1929. (1. 123.)

In this note, discussing the occurrence of *Calluna vulgaris* on Sable Island (Nova Scotia), the author disposes of an erroneous suggestion that the species was collected on the island by John Macoun in 1899. There seems little doubt that the heather is a recent adventive on Sable Island. It was first gathered there in 1911, by H. T. Güssow, and is now well established. The plant sprang up near trees which were imported from a French nursery, soon after their planting in 1901, and in all probability was used for, or carried in, the protective packing round the trees.

391. Mackenzie, K. K. "Some *Juncus* names." *Bull. Torr. Bot. Club*, **56**, pp. 25-32. 1929. (1. 124.)

The author discusses the nomenclature of some North American species of *Juncus*. He considers that the name *J. bicornis* should be used for the common rush generally known as *J. tenuis*; the name *J. tenuis* rightfully belongs to a United States species, usually called *J. dichotomus*. Further, he shows that the name *J. canadensis* should be applied to the species commonly known as *J. brevicaudatus* (or *J. coarctatus*), and for the plant which has been treated as *J. canadensis* proposes the new combination *J. longicaudatus* (based on *J. canadensis* var. *longicaudatus*).

392. Svenson, H. K. "Contributions from the Gray Herbarium of Harvard University—No. LXXXVI. Monographic Studies in the Genus *Eleocharis*." *Rhodora*, **31**, pp. 121-135, 152-163, 167-191, 199-219, 224-242, Plates 188-191. 1929. (1. 125.)

A paper dealing with the taxonomy and geographical distribution of the genus *Eleocharis*. Several of the series are treated in detail, with keys to the species. New species, varieties, and forms are proposed, and new combinations made. A number of Canadian species are concerned.

(2) SOUTH AFRICA (COLLABORATOR, A. W. EXELL)

393. Marloth, R. "Remarks on the Realm of the Cape Flora." *S. Afr. Journ. Sci.* **26**, pp. 154-159. 1929. (2. 79.)

The Cape Flora is discussed under the following headings: I. The historical development of views on the delimitation of the region. II. The geological evidence available concerning the south-western flora. III. The causes that have brought about the present composition of the vegetation.

There are no fossil records of angiospermous plants in South Africa, *Stangeria*, *Encephalartos*, and *Podocarpus* or *Widdringtonia* being the only genera of flowering plants represented in the Uitenhage beds. Hence theories must be based on the present distribution of plants in the southern hemisphere and the floral elements of the south-western region may be roughly arranged in three groups, namely: (1) the old Cape element, the remains of a former much more widely distributed southern, perhaps partly antarctic, flora; (2) elements

belonging to the old African flora still predominant in other parts of South and Tropical Africa; (3) post-Tertiary immigrants from the northern hemisphere. Examples of the three groups are given: the first-named group is much the largest.

The causes of the richness of the endemic flora are said to be: (1) the great diversity of topographical and physiographic features, and (2) the climatic conditions, past and present, which have produced a so-called "physiological isolation."

394. **Compton, R. H.** "The Flora of the Karroo." *S. Afr. Journ. Sci.* 26, pp. 160-165. 1929. (2. 80.)

The Karroo is encircled by floras of two main types—the Northern, linked directly with that of Central Africa, and the Southern or Cape flora. The elements of the Karroo flora are selected from these two types and are not related to those of other desert regions in North Africa or Australia. The two factors which the vegetation must necessarily be able to withstand are aridity and grazing, both of which act by destroying the aerial portions of the plants. The principal Karroo adaptations are thus succulence, geophily, regeneration, unpalatability, possibly disguise, and what may be called resurrectionism. Examples of these are given and it is shown how members of various families have contributed to the flora. A comparison is made with other desert and semi-desert areas.

395. **Phillips, E. P.** "A Brief Sketch of the Flora of the Environs of Pretoria." *S. Afr. Journ. Sci.* 26, pp. 184-189. 1929. (2. 81.)

The dicotyledonous vegetation of the neighbourhood of Pretoria is analysed in various ways and its affinities discussed. The general relationship is said to be with the Kalahari flora, the chief difference being in the greater percentage of Rubiaceae, Euphorbiaceae and Anacardiaceae. The flora differs considerably from that of the eastern mountain region, particularly in the dominance of such important tropical families as Rubiaceae, Euphorbiaceae and Acanthaceae, and the much higher percentage of Leguminosae is also significant. Isolated species from the mountainous region of eastern Transvaal are found on the banks of streams.

396. **Vedoorn, Inez C.** "Notes on the Vegetation of the Fountains Valley, Pretoria." *S. Afr. Journ. Sci.* 26, pp. 190-194. 1929. (2. 82.)

Fountains Valley is a deep, well-wooded valley which cuts the range of hills to the south of Pretoria. The vegetation was examined at different seasons of the year and lists of species in flower during different months are given.

397. **Roux, E. R.** "Observations on *Marsilia macrocarpa* Presl." *S. Afr. Journ. Sci.* 26, pp. 311-317, Text-figs. 1-9. 1929. (2. 83.)

The various growth-forms of *M. macrocarpa*, the only species of the genus found in South Africa, are described.

398. **van der Byl, P. A.** "Descriptions of some previously unnamed South African Fungi, V." *S. Afr. Journ. Sci.* 26, pp. 318-319. 1929. (2. 84.)

New species of *Thyriopsis*, *Phyllosticta*, *Coryneum*, *Peziza*, *Lembosia* and *Parasterina* are described.

399. **Fantham, H. B.** "Some Protozoa found in certain South African Soils, IX." *S. Afr. Journ. Sci.* 26, pp. 402-422. 1929. (2. 85.)

This paper contains further records of Protozoa found in soils from Cape Province, Orange Free State, Transvaal and Natal. The series of papers concludes with a general survey in which such subjects as seasonal variation, correlation with types of vegetation and effect of veld burning are dealt with.

400. Bremekamp, C. E. B. "A Revision of the South African Species of *Pavetta*." *Ann. Transv. Mus.* **13**, pp. 182-213, Plate V and Map. 1929. (2. 86.)

The genus *Pavetta* (Rubiaceae) is fully described and there is given a key to the sections, sub-sections and species occurring in South Africa. The geographical distribution of all the species is indicated and many new ones are described. In the introduction there is an account of symbiosis with bacteria occurring in the leaves of some species with striking resemblance to the bacterial nodules on the roots of leguminous plants.

401. Bremekamp, C. E. B. "*Stylocoryne* W. et Arn., a new Genus for the Flora of Africa." *Ann. Transv. Mus.* **13**, pp. 214-215. 1929. (2. 87.)

Several African species formerly placed in *Pavetta* are transferred to the genus *Stylocoryne* W. et Arn. hitherto only known from India and the Malay Archipelago. One new species from Transvaal is described.

402. Levyns, Margaret R. "Veld-burning Experiments at Ida's Valley, Stellenbosch." *Trans. Roy. Soc. S. Afr.* **17**, pp. 61-92, Text-figs. 1-10, Plates I-IV. 1929. (2. 88.)

The area chosen for the experiments was the northern slope of a secluded valley near Stellenbosch covered with dense Rhenosterveld, of which the dominant plant is *Elytropappus Rhinocerotis* Less. The vegetation is carefully classified and the various species listed according to their abundance. The area was divided into six plots, three of which were burned, one cleared and one left as a control (one plot was abandoned). The further history of the plots is discussed in detail. The experiment showed: (1) Rhenosterveld is not a stable type of plant community but is probably a protracted stage in succession; (2) burning leads to the rapid increase of the Rhenoster bush and other plants and also induces vigorous growth of a temporary nature among the petaloid monocotyledons and some other plants; (3) clearing does not favour the rapid increase of the Rhenoster bush and vigorous growth is more apparent among the grasses than among the petaloid monocotyledons.

403. Phillips, J. F. V. "The Influence of *Usnea* sp. (near *barbata* Fr.) upon the supporting Tree." *Trans. Roy. Soc. S. Afr.* **17**, pp. 101-107. 1929. (2. 89.)

The influence of a species of *Usnea* on *Podocarpus Thunbergii* Hook. (*P. latifolia* R. Br.) and *P. elongata* Carr. was investigated and the following conclusions arrived at: (1) the lichen is definitely detrimental, in that its fungal component is parasitic upon the tissues external to (and sometimes internal to) the cork-cambium. Vigorous crowns may be infected as well as defective ones. (2) The lichen cannot develop luxuriantly under the conditions of light, temperature, and humidity holding in undisturbed high forest, but grows apace when these factors are suddenly and severely altered by heavy exploitation. (3) Preservation of the forest canopy in primeval forest would seem to be the best means of inhibiting the rampant development of the lichen.

404. Schonland, S. "Material for a Critical Revision of the Crassulaceae. (The South African Species of the Genus *Crassula* L. (emend. Schonl.).)" *Trans. Roy. Soc. S. Afr.* **17**, pp. 151-293. 1929. (2. 90.)

The paper consists of a classification of the South African species of *Crassula* in natural groups with remarks on their possible phylogeny. A key to the species is given together with their geographical distribution and phylogeny.

405. Duthie, A. V. "The Species of *Isoetes* found in the Union of South Africa." *Trans. Roy. Soc. S. Afr.* **17**, pp. 321-332, Text-figs. 1-7, Plates XI-XII. 1929. (2. 91.)

A key is given to the five species of *Isoetes* found in the Union of South Africa, three of which are here described for the first time.

406. Brown, N. E. "Contributions to a Knowledge of the Transvaal Iridaceae." *Trans. Roy. Soc. S. Afr.* **17**, pp. 341-352. 1929. (2. 92.)

This paper deals with the Transvaal species of the four genera *Dietes*, *Helixyra*, *Morea* and *Homeria*, and is an attempt accurately to delimit the group of Irids known as "tulps," many of which are very poisonous to cattle. The paper contains several new species and new combinations.

407. Fritsch, F. E. and Rich, Florence. "Contributions to our Knowledge of the Freshwater Algae of Africa. 7. Freshwater Algae (exclusive of Diatoms) from Griqualand West." *Trans. Roy. Soc. S. Afr.* **18**, pp. 1-92, Text-figs. 1-32. 1929. (2. 93.)

This paper contains an enumeration of the freshwater algae (excluding diatoms) collected in Griqualand West, a region of which the algal vegetation has not been hitherto described. A number of new species are described.

408. Fritsch, F. E. and Rich, Florence. "Contributions to our Knowledge of the Freshwater Algae of Africa. 8. Bacillariales (Diatoms) from Griqualand West." *Trans. Roy. Soc. S. Afr.* **18**, pp. 93-123, Text-figs. 1-11. 1929. (2. 94.)

The diatoms present in the samples from Griqualand West that formed the subject of the preceding contribution are here dealt with. Owing to the small range of habitats the number of species recorded is said to be surprisingly small. A few new species and varieties are described.

409. Dixon, H. N. and Wager, H. A. "New and Noteworthy Mosses from South Africa." *Trans. Roy. Soc. S. Afr.* **18**, pp. 247-261, Plate III. 1929. (2. 95.)

A number of new species are described and new records given. Among the latter is the interesting discovery of *Jaegerina stolonifera* C.M. belonging to a small genus of six species, of which three are confined to the Mascarene Islands (including Madagascar), one species is confined to Jamaica, one to the Philippines and one, the present one, occurs in South India, the Mascarenes and South Africa.

410. Brown, N. E. "*Mesembryanthemum* and Allied Genera." *Journ. of Bot.* **67**, pp. 17-20. 1929. (2. 96.)

411. "Novitates Africanæ." *Journ. of Bot.* **67**, pp. 132-139. 1929. (2. 97.)

This contains descriptions of new species of *Gladiolus*, *Watsonia*, *Gethyllis*, *Forbesia*, *Haworthia* and *Erica* by Mrs L. Bolus and one species of *Watsonia* by Mathews and L. Bolus.

412. "Decades Kewenses." *Bull. Misc. Inf. Kew*, pp. 4-12. 1929. (2. 98.)

This contains a new genus, *Catalepis* Stapf and Stent, containing one new species, *Catalepis gracilis* Stent and Stapf, from the Transvaal.

413. Brown, N. E. "New Species of and Critical Notes on *Mesembryanthemum* and Allied Genera." *Bull. Misc. Inf. Kew*, pp. 56-62. 1929. (2. 99.)

This contains descriptions of new species in the genera *Glottiphyllum*, *Lithops*, *Mesembryanthemum* and *Psilocaulon*, and also new combinations in the genera *Dorotheanthus*, *Echinus*, *Mentocalyx* and *Vanzijlia*.

414. Smith, C. A. and Hubbard, C. E. "Notes on African Grasses. IX. Some Saline-loving Grasses occurring in South Africa." *Bull. Misc. Inf. Kew*, pp. 83-87, 1 text-fig., Plate IV. 1929. (2. 100.)

Seeds of *Mesembryanthemum crystallinum* L., *M. geniculiflorum* L., *Galenia sarcophylla* Fenzl., *Atriplex capensis* Moq., *Salsola strobiliformis* C. A. Sm. and *Hypertelis verrucosa* Fenzl., all salinaceous plants, were sown on an area of heavily saline soil on the "Bakbank Farm" in the Fauresmith Division, Orange Free State. The area was allowed to develop undisturbed, and on the passing of the second growing season the influx of several grasses, *Puccinellia angusta* (Nees) Smith and Hubbard, *Bromus unioloides* H.B.K. and *B. japonicus* Thunb., was noticed. The first-named became very luxuriant, although it had never before been found growing in the saline areas of the Fauresmith Division. A new species of *Puccinellia* is described and figured.

415. Hubbard, C. E. "Notes on African Grasses. XI. A New Genus of Grasses from Bechuanaland." *Bull. Misc. Inf. Kew*, pp. 319-322. 1929. (2. 101.)

A new genus of grasses, *Megaloprotachne* Hubbard, belonging to the *Digitariastrae* is described from Bechuanaland.

416. Schwantes, G. "Neue Mesembriaceen. IV." *Monatsschr. Deutsch. Kakteen-Gesell.* 1, pp. 14-17. 1929. (2. 102.)

Descriptions of new species of *Hereroa*, *Mitrophyllum*, *Nelia* and *Schlechteranthus* are given.

417. Tischer, A. "*Faucaria Haagei* Tisch. spec. nov." *Monatsschr. Deutsch. Kakteen-Gesell.* 1, pp. 20-21, 1 photograph. 1929. (2. 103.)

418. Schwantes, G. "*Argyroderma* N. E. Br." *Monatsschr. Deutsch. Kakteen-Gesell.* 1, pp. 27-32, 2 Text-figs. 1929. (2. 104.)

This includes a description of a new species of the genus *Agyroderma*.

419. von Poellnitz, K. "Standorte von *Haworthia*- und *Apicra*-Arten." *Monatsschr. Deutsch. Kakteen-Gesell.* 1, pp. 38-41. 1929. (2. 105.)

Localities are given for various species of *Haworthia* and *Apicra*.

420. Pieper, W. "Beiträge zur Flora von Afrika. LV. Vorarbeiten zu einer Revision der afrikanischen *Vitex*-Arten mit Berücksichtigung der übrigen." *Engl. Bot. Jahrb.* 62, Beibl. 141, pp. 1-91, Plates VIII-XII. 1929. (2. 106.)

This systematic account of the African species of the genus *Vitex* includes a few South African species which are placed in the sub-genus *Holmskioldiopsis* Pieper.

421. Muir, J. "The Vegetation of the Riversdale Area, Cape Province." *Botanical Survey of South Africa*, Memoir No. 13, pp. 1-82, 1 Map. 1929. (2. 107.)

The Riversdale area is divisible into four regions differing geologically and botanically: (1) The Strandveld, known popularly as the "Duine." (2) The Renosterveld, known as the



"Hardeveld" or "Middelveld." (3) The Langebergen, usually termed the "Langeberg."  
(4) The Klein Karoo, usually called simply the "Karoo."

(1) *The Strandveld*. This is the coast belt extending for about 44 miles from the Gouritz River to the Duivenhoeks River and consisting mainly of fixed sand intersected with rocky ridges and outcrops of limestone. Near the coast are mobile sand dunes. The region as a whole is pleasant, beautiful and fertile with an abundance of flowering shrubs and entomophilous herbs. The area is carefully subdivided and the various associations dealt with in detail. *Scaevola Thunbergii* is particularly characteristic of the sandy foreshore, where it builds considerable hillocks. At the summit of the mobile dunes such plants as *Rhus crenata*, *Metalasia muricata*, *Passerina rigida* and *Stoebe cinerea* are locally dominant. In the valley at the base of the dunes there are shrubs and small trees, of which the commonest are *Sideroxylon inerme*, *Gymnosporia laurina* and *Mystroxydon sphaerophyllum*. Between the dune valley and the limestone hills are sandy coast flats whose principal shrubs are *Pterocelastrus variabilis*, *Rhus glauca*, *Gymnosporia laurina*, *Cullumia setosa*, etc. There are also various saline areas which have characteristic vegetation. In the inland region of the Strandveld the vegetation is mainly of a xerophilous type and is rich in Ericaceae, Rutaceae and Proteaceae. The river valleys of the region are clothed in a dark green mass of vegetation with *Sideroxylon inerme*, *Schotia speciosa* and *Aloe arborescens* occurring in abundance, while on an alluvial area at Elberts Kraal *Acacia karoo* is abundant.

(2) *The Renosterveld*. This lies between the Strandveld and the Langebergen in the middle of the district: it is characterised by gently undulating hills and valleys, and is fairly well watered. The vegetation contrasts strongly with that of the Strandveld, the Proteaceae, Ericaceae and Restionaceae becoming scarcer as one goes northwards and *Sideroxylon inerme* almost entirely disappearing. The vegetation is of a sclerophyllous type with *Elytropappus Rhinocerotis*, a xerophytic shrub belonging to the Compositae, dominant. In the Renosterveld area proper *Relbunium genistaeifolia* and the grasses *Cynodon Dactylon* and *Themeda Forskalii* are often sub-dominant, and the three great geophytic families of Monocotyledons are well represented owing to centuries of veld burning. The Aloe Scrub, confined to the hill slopes of the eastern half of the Division, is being rapidly cleared away, except on rocky ground. The characteristic species are *Aloe ferox*, *A. arborescens* and *A. Salmdyckiana*, while *Sideroxylon inerme* and *Cussonia spicata* are common trees in the scrub. Species of *Rhus* and several Celastraceae are represented, also several succulents and such climbers as *Asparagus* spp. and *Sarcostemma viminalis*. A marked feature is the number of species with thorns. *Acacia karoo* occurs in the river valleys of the Renosterveld.

(3) *The Langebergen*. This is a mountain range running roughly east and west and belonging to the Table Mountain series, some of the mountain summits being plateaux 4000 ft. above sea-level. The Lithophyte Succession is said to be similar to that of the Drakensberg. Associations of Cyanophyceae represent the first stage. These are followed by lichen associations which are in turn followed by mosses and hepatics. The first phanerogamic species are *Crassula rubricaulis*, *C. punctulata* and *Mesembryanthemum deltoides*. The principal sclerophyllous types of vegetation are Heath and Macchia. The former is a stage in the succession to Macchia and is situated on the rounded foothills and lower mountain slopes. Species of *Erica* are dominant and the smaller genera of the family Ericaceae are well represented. The heath passes insensibly into true macchia, known in South Africa as "fynbos" and closely related ecologically to the macchia of the Mediterranean region and to the chaparral of California. The vegetation consists of a multitude of woody evergreen shrubs, usually with leaves much reduced in size. Some of the most frequent and striking species are *Protea neriifolia*, *P. latifolia*, *P. longiflora*, *Cliffortia ilicifolia* and *Leucadendron strictum*. The prevailing families are Restionaceae, Proteaceae, Ericaceae, Geraniaceae, Compositae and Leguminosae. Forest is found usually in ravines and rocky sites, mostly of southern aspect. The principal trees and large shrubs are *Cunonia capensis*, *Curtisea faginea*,



*Olea laurifolia*, *Hartogia capensis*, *Royena lucida*, *Gymnosporia acuminata*, *G. buxifolia*, *Pterocelastrus variabilis*, *Scolopia Mundii*, *Apodytes dimidiata*, *Olinia cymosa*, *Podocarpus latifolia*, *Burchellia capensis* and in some woods *Gardenia Rothmannia*. The composition corresponds closely to that of sub-tropical high forest in the Knysna division.

(4) *The Klein Karoo*. This lies to the north of, and parallel with the Langebergen, extending for about 40 miles from east to west and 6 to 8 miles from south to north. It is an undulating plain with stony ridges and rocky hills, from 1000 to 1700 ft. in altitude, intersected by water-courses which are dry except after rains. The general aspect is desert-like with scattered shrubs and intervening bare areas of hard, baked ground. The vegetation is mainly succulent and xerophytic with a large proportion of geophytes, but with a few annuals which come up after rain. The mountain macchia is bordered by a narrow strip in which *Elytropappus Rhinocerotis* is dominant. *Euclea undulata* is the commonest shrub in this belt, and *Rhus lancea* comes next in order of frequency. The succulent families Euphorbiaceae, Crassulaceae and Aizoaceae are well represented. Travelling northwards *Elytropappus* becomes scarcer, and *Salsola aphylla* becomes abundant. Three arborescent species of *Cotyledon* are especially noteworthy and many species of *Mesembryanthemum* are to be found. *Galenia africana* is sometimes dominant. On hills near the Langebergen *Euclea undulata* is the dominant shrub, but some hills are thickly covered with *Aloe microstigma*. Further inland *Carissa Arduina* and *Portulacaria afra* often occur with the still dominant *Euclea undulata*. Annuals are, to some extent, an index to aridity, becoming more prominent according to increased dryness. The "quartz" fields show an interesting and largely peculiar vegetation in which "mimetic" plants are characteristic, but no useful purpose seems to be served by this "mimicry." Along the river-courses the trees are larger, the chief being *Acacia karoo*.

(3) AUSTRALIA AND TASMANIA (COLLABORATOR, V. S. SUMMERHAYES)

422. **Pescott, E. E.** *The Orchids of Victoria*, pp. 97, 1 coloured and 16 photographic plates. The Horticultural Press Pty. Ltd., 78a, Victoria Street, Melbourne. 1928. 6s. (3. 28.)

Descriptions of the species are supplied with partial keys to some of the genera. Notes on geographical distribution, etc., accompany the descriptions. A number of the species are illustrated.

423. **Lucas, A. H. S.** "Census of the Marine Algae of South Australia." *Trans. Roy. Soc. S. Australia, Adelaide*, 53, pp. 45-53. Dec. 24th, 1929. (3. 29.)

340 species are recorded, of which 250 belong to the Rhodophyceae. The distribution of the species is given according to regions. Most of the records are from the east of Investigator Strait.

424. **Prescott, J. A.** "The Vegetation Map of South Australia." *Trans. Roy. Soc. S. Australia, Adelaide*, 53, pp. 7-9, 2 maps. Dec. 24th, 1929. (3. 30.)

A vegetation map of South Australia has been prepared based on the records of the Lands and Survey Department. A simplified and reduced map (No. 2) prepared from this is included in this paper. The distribution of the main types of vegetation is marked.

425. **Ostenfeld, C. H.** "A List of Australian Sea Grasses." *Proc. Roy. Soc. Victoria, Melbourne*, 42, pp. 1-4. Oct. 9th, 1929. (3. 31.)

Fifteen species belonging to the families Potamogetonaceae and Hydrocharitaceae are enumerated, with records of distribution based on specimens seen.

426. Morris, P. F. "Ecology of Marysville and Lake Mountain." *Victorian Naturalist*, Melbourne, 46, pp. 34-42, 1 plate. June 10th, 1929. (3. 32.)

The area described is a mountainous region in the neighbourhood of the Dandenong Range. In the lower areas *Nothofagus cunninghamii* is locally dominant along the river banks, while elsewhere eucalypts are the chief trees. *E. viminalis*, *E. ovata* and *E. rubida* are the commonest species, the former being chiefly by the rivers. Species of *Acacia*, shrubs and herbaceous plants are found under the eucalypts, but are less common under the *Nothofagus*.

The vegetation of the Lake Mountain can be divided into three main parts, viz.: (1) Basal Slopes, on which the ground is often boggy and supports there only herbaceous vegetation. (2) Hillsides, covered chiefly with open forest with thick undergrowth. (3) Echo Flat, a high swamp in which *Eucalyptus coriacea* is the only tree, occurring on the margins. A list of all the species found on Echo Flat is given.

On the mountains below, forests of various species of *Eucalyptus* occur.

427. Rupp, H. M. R. "Forms and Habits of Certain Orchids." *Victorian Naturalist*, Melbourne, 46, pp. 3-8. May 4th, 1929. (3. 33.)

A number of peculiar biological features found in various Australian orchids are here described and discussed. These are as follows: (1) The occurrence of giants and dwarfs in certain species. (2) Elongation of the flowering stem after fertilisation. (3) Anomalies of habitat. (4) Anomalies of the flowering season. (5) Habits in connection with basal leaves of terrestrial species.

428. Sutton, C. S. "A Sketch of the Vegetation of the Cradle Mountain, Tasmania, and a Census of its Plants." *Papers and Proc. Roy. Soc. Tasmania*, Hobart, 1928, pp. 132-159. March 11th, 1929. (3. 34.)

Cradle Mountain, together with two adjacent mountains, consists of the remains of a dolerite sill, and rises to just over 5000 ft. (1500 m.) above sea level. Glacial indications are to be seen everywhere, while there are numerous lakes in the vicinity. The annual rainfall at 3000 ft. (900 m.) is high, reaching nearly 135 in. in 1924, the wettest months being in the winter. The range of temperature is considerable and frost may occur in any month. Humidity is high, the means ranging between 67 and 95 per cent.

The following plant communities are recognised:

(1) Forest, consisting of four types: (a) *Athrotaxis-Nothofagus* forest occupying the higher slopes on the west side and dominated by *Athrotaxis selaginoides*, *Nothofagus cunninghamii* being the next important tree; (b) open forest, lying between (a) and grassland on the lower slopes, and composed chiefly of *Eucalyptus muelleri*; (c) *Eucalyptus-Athrotaxis* forest on east and south sides of Dove Lake, and composed of the species already mentioned; (d) *Eucalyptus-Nothofagus* forest on steep slopes near Crater Lake, a rather open low type in which the dominant is *Eucalyptus coccifera*.

(2) Dwarf subalpine scrub, occurring at the lower end of Cradle Valley. A number of species are co-dominant forming a thickset growth about 12-18 in. high.

(3) The *Gymnoschoenus* (button grass) association occupies most of the sour ground in the valley. A number of small herbaceous species are associated with the button grass. This community covers large areas in many other parts of Tasmania.

(4) The *Gleichenia-Restio* association occurs on wet ground.

(5) Subalpine meadow covers the lower slopes of the mountain. *Poa caespitosa* is the chief species, forming close tussocks.

(6) Aquatic and bog plants.

(7) Subantarctic fell-field. This occurs on the plateau at or above 4000 ft. (1200 m.). The ground is very diversified, being very rocky in places, while there is but little soil anywhere. In the summer months aridity sometimes occurs owing to rapid run off of the water. The chief growth-form is the cushion or "boulder" type, but mat types and prostrate espalier types are also found. The chief species giving character to the vegetation are *Dracophyllum minimum*, *Donatia novae-zelandiae*, *Ewartia meredithae* and *Pterygopappus lawrencii*. These act as seed beds in which other smaller species can become established. Among rocks and boulders low scrub is found.

A short comparison of the floras of Cradle Mountain and of the Australian Alps is made. A complete list of the species recorded with their "communal" distribution is furnished.

429. Wood, J. G. "Floristics and Ecology of the Mallee." *Trans. Roy. Soc. S. Australia, Adelaide*, 53, pp. 359-378, 1 text-fig., 1 map. Dec. 24th, 1929. (3. 35.)

The area studied includes north-west Victoria, south-west New South Wales and various parts of South Australia. Mallee scrub is dominated by eucalypts of a definite habit, the most important species being *Eucalyptus dumosa*, *E. oleosa* and *E. gracilis*. All are small trees from 2-12 m. in height, and bearing several sparingly branched stems from an underground root stock. A regular canopy is formed at the apices of the branches. Various xerophytic shrubs also occur, while the ground flora consists chiefly of ephemerals.

A map shows the more exact distribution of the mallee area. The mallee occurs only between the 8 in. and 20 in. rainfall isohyets, the rain all falling during the winter. Variability from the average amount of rainfall is 15-20 per cent. All the soils are of "Solonetz" type, consisting of sands and silt over nodular travertine limestone. They are invariably alkaline with a saturation percentage between 32 and 38. The surface soils have usually a pH of about 7.5-7.7, and the subsoils one of about 7.7-8.0.

About 600 species have been recorded from the mallee area. An analysis of these species shows that only about 25 per cent. are confined to the region, the remainder being found either to the north or south, but few in both directions. Analyses of the floras of the main mallee sub-areas are given. A spectrum of the life forms according to Raunkiaer's method show that nanophanerophytes, chamaephytes and therophytes are particularly common compared with the "normal" spectrum, while the percentage of hemicryptophytes is low.

More detailed descriptions of certain mallee areas follow. Few definite communities can be recognised, but locally the eucalypts are replaced by species of *Callitris* or by *Casuarina lepidophloia*. The occurrence of these communities depends on slight differences in the edaphic factors. On Kangaroo Island the dominant mallee species is *Eucalyptus cneorifolia*. On the whole the mallee region is transitional between the savannah forests of the southern wetter districts and the northern salt bush and mulga communities. A list of the species recorded is given with growth-form in each case and more detailed distribution.

430. Francis, W. D. *Australian Rain-Forest Trees, excluding the Species confined to the Tropics*, pp. xi + 137, 25 text-figs., 213 half-tone illustrations, 1 map. A. J. Cumming, Government Printer, Brisbane. 1929. 10s. (3. 36.)

Rain forest occurs at places down the eastern Australian seaboard from Cape York to Cape Otway, and also in Tasmania. It is found in the coastal districts and never penetrates more than 100 miles inland. The greatest areas are in Queensland, but there are some considerable areas in northern New South Wales.

The forests may be divided arbitrarily into two types, namely, those north of latitude 29° S. which are tropical in character and those south of this line which show increasingly

characters of temperate rain forest. South of latitude 33° S. the tropical element has mostly disappeared.

Most of the rain forests occur in regions with 60 in. or more annual rainfall. Although the forests occur on many soil types, many large areas are found on basalt soils which are favourable for development of rain forest. The forests are very sensitive to fire and are easily destroyed by burning, but owing to the high humidity this does not often occur in nature. The size of the trees and the occurrence of buttresses is also noted. Many of the trees develop buttresses when quite young, and before exposed to the bending effects of winds, etc. Flanged stems, corrugated woody cylinders, bark, timber and the leaves of various species are also discussed.

The species are described in detail with ecological and economic notes and geographical distribution. Many of the more important ones are illustrated. There is a general artificial key to facilitate identification, while in each family there is a key to the genera included.

(4) NEW ZEALAND (COLLABORATOR, V. S. SUMMERHAYES)

431. Cockayne, L. "The Vegetation of New Zealand." *Die Vegetation der Erde, Leipzig*, 14, ed. 2, pp. xxvi + 456, 87 plates, 3 maps. 1928. 42s. (4. 29.)

In the introduction (Part I) is a history of the botanical exploration of New Zealand from Cook's discovery up to 1927. This is followed by a general account of the physiography and then of the climate.

Part II deals with the primitive and semi-primitive vegetation. This is dealt with under four main divisions, viz. the vegetation of (i) the sea coast, (ii) lowlands and lower hills, (iii) high mountains, (iv) the outlying islands. In the first three sections general observations come first, followed by chapters on leading physiognomic plants and their life forms, and the autecology of the respective plants.

(i) The communities are dealt with seriatim as follows: (1) Communities of Salt and Brackish water; (2) Salt meadows; (3) Seashore communities; (4) Dunes; (5) Rock and Cliff vegetation; (6) Coastal scrub; (7) Coastal forest.

(ii) The following communities are recognised in this region: (1) Forest consisting of (a) Subtropical rain forest of broad-leaved trees and conifers, and (b) Subantarctic rain forest. (a) is divided into three main series: (a) Kauri forest, dominated by *Agathis australis*; (β) Podocarp-broad-leaved dicotylous forest on dry ground; (γ) Podocarp-broad-leaved dicotylous forest on wet ground. Under (b) various types of *Nothofagus* forest are described. (2) Shrubland and fernland. (3) Water associations. (4) Swamp vegetation. (5) Bog vegetation. (6) River-bed vegetation. (7) Grassland, consisting of low tussock grassland dominated by *Festuca novae-zelandiae* and *Poa caespitosa*, and tall tussock grassland in which *Danthonia raoulii* is dominant. (8) Rock vegetation.

(iii) The communities recognised in this region are as follows: (1) Subalpine forests, the most important of which are types dominated by various species of *Nothofagus*, other types being dominated by subtropical species. (2) Shrub communities; these are formed chiefly of species of *Olearia*, *Senecio*, *Hebe*, *Coprosma* and *Dracophyllum*. (3) Rock vegetation. (4) Vegetation of loose stony debris. (5) Fell-field. (6) Grassland, much the same types as before. (7) Herb-field dominated by large mesophytic herbs. (8) Herb-moor, intermediate between herb-field and bogs.

(iv) The outlying islands are considered under the following headings: (a) Kermadec Islands; (b) Chatham Islands; (c) the Subantarctic Islands.

In Part III the effect of settlement upon the plant covering of New Zealand is discussed. The new vegetation produced is classified into four categories: (1) Modified vegetation, in

which slight changes have taken place in the primitive communities; (2) Exotic-induced communities, formed from introduced plants; (3) Indigenous-induced communities, that is, entirely fresh communities consisting of native plants; (4) Artificial communities, such as pastures, etc. There is a final chapter on Agriculture and Horticulture in New Zealand.

Part IV deals with the flora of New Zealand, its distribution and composition. The area is first divided into botanical provinces, and these are again subdivided into botanical districts which are described and characterised in general terms. Subdistricts are recognised in some districts.

The various elements of the flora are discussed and the following groups are recognised: (1) Endemic; (2) Palaeozelandic; (3) Australian; (4) Subantarctic; (5) Palaeotropic; (6) Cosmopolitan.

In Part V the history of the flora is considered.

432. Allan, H. H. *New Zealand Trees and Shrubs, and How to Identify Them*, pp. vi + 188, frontispiece and 28 figs., mostly photographs, 2 maps. Whitcombe and Tombs, Ltd., New Zealand, Melbourne and London. 1928. 6s. 6d. (4. 30.)

This is a tree and shrub flora of New Zealand. The text is arranged on the key system, so that it is possible to name the species by vegetative characters only. Short descriptions of all the species are given with distribution and habitat notes. A key to the genera based on floral characters is given at the end. The Introduction contains notes on genera and species, growth forms, characteristics of leaves, and hints to collectors. This book is of pocket size and easily carried in the field. There are excellent photographs of some of the species.

433. Oliver, W. R. B. "A Revision of the Genus *Dracophyllum*." *Trans. New Zealand Institute, Wellington*, 59, pp. 678-714, Plates 78-102. March 25th, 1929. (4. 31.)

The total number of species recognised is forty-five, while nine hybrids are also included. A synopsis of the species is first given, followed by short descriptions, geographical distribution and ecological notes. There are photographs of twenty-five of the species.

434. Laing, R. M. and Oliver, W. R. B. "The Vegetation of the Upper Bealey River Basin, with a list of the Species." *Trans. New Zealand Institute, Wellington*, 59, pp. 715-730. March 25th, 1929. (4. 32.)

The flora of the district is poor in species as a result of the following factors: (1) high evaporation rate; (2) lack of soil; (3) low winter temperature; (4) frequent heavy gales; (5) prejudicial effect of beech forest on the germination of seedlings. Each of these factors is discussed in greater detail. The following plant formations are very briefly described, viz. forest, scrub, tussock grassland, bogs, cushion-plant communities, meadow, fell field and reed swamp. A full list of the species recorded is given.

(5) PACIFIC ISLANDS (COLLABORATOR, V. S. SUMMERHAYES)

435. Greenwood, W. "The Food Plants or Hosts of Some Fiji Insects, III." *Proc. Linn. Soc. New South Wales, Sydney*, 54, pp. 344-352. Oct. 25th, 1929. (5. 8.)

Further records supplementing the two earlier papers are given.



(7) INDIA, BURMA AND CEYLON (COLLABORATOR, R. J. D. GRAHAM)

436. "Calophyllum." "Evergreen Forests in British Malabar." *Indian Forester, Allahabad*, 55, pp. 20-30, Jan. 1929. (7. 66.)

A paper submitted to compete for the Brandis Prize giving an historical and ecological account of this specialised and local type of forest. The commonest species belong to *Mesua*, *Calophyllum* and *Cullenia*. The writer emphasises the slow regeneration where the forest is disturbed and outlines a plan by which the forests which were reserved till 1919 can be worked.

437. Sweet, J. M. "Natural Regeneration of *Adina cordifolia*." *Indian Forester, Allahabad*, 55, pp. 40-42, Plate 1. Jan. 1929. (7. 67.)

A successful experiment to test the possibility of regeneration of *Adina* after burning in the Mount Stuart Forests, Madras, is described.

438. Coffey, T. M. "Hill Taungyas in the Kurseong Division, North Bengal." *Indian Forester, Allahabad*, 55, pp. 80-85, Plates 2, 3. Feb. 1929. (7. 68.)

439. Warren, W. D. M. "Sal and its Regeneration." *Indian Forester, Allahabad*, 55, pp. 182-186. March, 1929. (7. 69.)

A criticism of Osmaston's paper "Sal and its Regeneration" (No. 353). The main points criticised are (1) drainage of subsoil which the writer thinks insufficiently emphasised, (2) burning as a method for establishing sal.

440. Sher Singh. "The Effect of Climate on the Conifers of Kashmir." *Indian Forester, Allahabad*, 55, pp. 189-203. April, 1929. (7. 70.)

Kashmir is defined as the upper portion of the Jhelum Valley. A comparison of the forest in this area with those outside is outlined. Outstanding differences are the absence of Deodar on the north slopes of Pir Panjal, the complete absence of *Chir* Pine, all Oaks, Laurels, low level Rhododendrons, *Pieris*, *Cornus*, *Carpinus*, *Alnus nitida* and many species of *Euonymus*, their place being taken by *Kail* and *Fir*. An explanation of these anomalies is offered on edaphic, climatic and topographical grounds. The paper concludes with a comparison of the distribution of the Blue Pine and the Spruce in Kashmir and British India.

441. Cowan, J. M. "The Malatas of Northern Bengal." *Indian Forester, Allahabad*, 55, pp. 226-231, Plate 10. April, 1929. (7. 71.)

A key based on leaf characters illustrated in the plate is given of *Mallotus Roxburghianus*, *M. philippinensis*, *M. nepalensis*, *M. albus*, *M. repandus*, *Macaranga pustulata*, *M. denticulata*, *M. Gamblei* and *M. indica*.

442. Gupta, B. L. "A new species of *Vateria*." *Indian Forester, Allahabad*, 55, pp. 231-232, Plate 11. April, 1929. (7. 72.)

*Vateria macrocarpa* is described as a new species.

443. Parker, R. N. "Indian Climbing Acacias of the Caesia Group." *Indian Forester, Allahabad*, 55, pp. 225-333. June, 1929. (7. 73.)

A key to the species and a description of a new species, *Acacia diadenia* Parker, is given.

444. Prim, Nath Kohli. "Adventitious Roots." *Indian Forester, Allahabad*, 55, pp. 371-372, Plate 14. June, 1929. (7. 74.)

A photograph of adventitious roots on *Pinus excelsa*.



445. Parker, R. N. "Two Anonaceous Trees from Burma." *Indian Forester, Allahabad*, 55, pp. 375-376, Plate 15. July, 1929. (7. 75.)

*Polyalthea crassa* Parker and *Sageraea bracteolata* Parker are described.

446. Champion, H. G. "The regeneration of Tropical Evergreen Forests." *Indian Forester, Allahabad*, 55, pp. 429-446, 480-495. Aug. and Sept. 1929. (7. 76.)

The paper opens with synecology of the rain forest followed by the distribution and composition of the tropical evergreen forest and the local forms displayed. The natural regeneration is described and suggestions are made to further this. Artificial regeneration offers serious difficulties on account of the nature of the ground where the forest occurs and the shade requirement of the young stages of its chief species. The marked deterioration on felling is emphasised unless appropriate cultural operations are undertaken.

447. De, R. N. "*Barringtonia acutangula*." *Indian Forester, Allahabad*, 55, pp. 498-502, Plate 21. Sept. 1929. (7. 77.)

An account of the germination of the water-borne seeds is given.

448. Smythes, E. A. "Sal and its Regeneration." *Indian Forester, Allahabad*, 55. Sept. 1929. (7. 78.)

A detailed description of the damage done by deer to sal is given. This factor was not dealt with by Osmaston (353).

449. Norris, Dorothy, Rangaswami, M., Vengupolan, M. and Ranganathan, S. "An Investigation into the Plant Requirements of *Zizyphus Jujuba* during Growth and Lac Cultivation, Part I." *Indian Forester, Allahabad*, 55, pp. 525-534, Plates 23-29. Oct., 1929. (7. 79.)

A contribution from the Indian Lac Research Institute giving the results of periodical analyses. Seasonal variation in total nitrogen content occurs, there being more in leaves collected in August than in January. This is correlated with a decrease and increase in the other organs. Both total and inorganic phosphorus and also potassium show a gradual fall with age. There is most phosphorus in the leaves and least in the roots. Seasonal variations in potash content of leaf, stem and root are noted and a connection with calcium variations is indicated.

450. Gorrie, R. MacLagan. "A Short Description of the Upper Bashahr Forest Division." *Indian Forester, Allahabad*, 55, pp. 534-540. Oct., 1929. (7. 80.)

A description dealing with a tongue of land running into the inner Himalaya between Kulu and the United Provinces included in the area is the Shipki Pass.

451. Blatter, E. "The Indian Bamboo brought up to date." *Indian Forester, Allahabad*, 55, pp. 541-562, 586-613. Oct. and Nov. 1929. (7. 81.)

A critical revision of the Indian bamboos following the arrangement of Gamble's monograph of the Indian bamboos (*Ann. Roy. Bot. Gard. Calcutta*, 7, 1896), concludes with a list of books consulted.

452. Turner, J. E. C. "West Almora Division." *Indian Forester, Allahabad*, 55, pp. 578-586, Plate 30. Nov., 1929. (7. 82.)

A description of an area in Kumaon United Provinces.

453. Gorrie, R. Maclagan. "A Destructive Parasite on the Himalayan Blue Pine." *Indian Forester, Allahabad*, 55, pp. 613-617, Plate 31. Nov., 1929. (7. 83.)

*Arceuthobium minutissimum* Hook. is described together with the life history and the damage to *Pinus excelsa*.

454. De, R. N. "The Regeneration of Tropical Evergreen Forests." *Indian Forester, Allahabad*, 55, pp. 620-623, Plate 32. Nov., 1929. (7. 84.)

A criticism of Champion's paper (446) dealing particularly with the tropical evergreen forests of Assam.

455. Parker, R. N. "*Leucana glauca*." *Indian Forester, Allahabad*, 55, pp. 641-642, Plates 33, 34. Dec. 1929. (7. 85.)

An account of experiments at Chandbagh.

456. Parker, R. N. "The Indian Species of *Nyssa* Linn." *Indian Forester, Allahabad*, 55, pp. 642-645. Dec. 1929. (7. 86.)

A key to the three Indian species is given with a description of *N. megacarpa* Parker, a new species.

457. Hall, W. F. "Ramnager Forest Division." *Indian Forester, Allahabad*, 55, pp. 645-651. Dec. 1929. (7. 87.)

A description of a tract in the United Provinces covering 300 miles in the foothills of the Himalayas. The area contains some of the finest sal forest in the Provinces.

458. Börgesen, F. "Notes on the Vegetation at Dwarka on the West Coast of India with reference to Raunkiaer's 'Life Forms' and Statistical Methods." *Journ. Ind. Bot. Soc. Madras*, 8, No. 1, pp. 1-18, Plates I-III. March, 1929. (7. 88.)

The notes are based on a stay of 8 days at Dwarka in Baroda and represent spare time occupation, the principal object of the stay being the rich algal flora. Notes on twenty-eight species of flowering plants arranged according to size are given. A comparison is made with six other tropical and subtropical localities. The conclusion is "on the whole the vegetation shows much likeness to the Canarian vegetation from the dry flats and hills and to the Mediterranean one and that not only as to the physiognomy but also as to the composition of the flora as a whole."

459. Blatter, E. "Revision of the Genus *Butea* Koen." *Journ. Ind. Bot. Soc. Madras*, 8, No. 2, pp. 133-138. July, 1929. (7. 89.)

The genus *Spatholobus* now disappears under *Butea* which had already expanded to include *Meizotropis*.

460. Blatter, E. "The Indian Species of *Ternmalia* Linn." *Journ. Ind. Bot. Soc. Madras*, 8, No. 4, pp. 245-262. Dec. 1929. (7. 90.)

The genus now includes twenty Indian species. A description of each with its localities is given.

461. **Sabnis, F. S.** "A Note on the Ecology of the Flora of Sind." *Journ. Ind. Bot. Soc. Madras*, **8**, No. 4, pp. 263-386. Dec. 1929. (7. 91.)

After statistical study of climate and flora the author briefly describes the following formations: (1) Halophytic or semi-halophytic; (2) Aquatic or semi-aquatic; (3) Kalar soil; (4) Sand; (5) Gravel; (6) Rock; (7) Ruderal.

The author ventures the predictions that the whole flora of the Sind desert will in course of time assume western characters owing to invasions from the western deserts.

462. **Alston, A. H. G.** "Names published in Moon's Catalogue." *Ann. Roy. Bot. Gard. Peradeniya, Ceylon*, **11**, Part 2, pp. 203-206. March, 1929. (7. 92.)

Twenty-one new names are given.

463. **Alston, A. H. G.** "The Flora of Maragalakande." *Ann. Roy. Bot. Gard. Peradeniya, Ceylon*, **11**, Part 2, pp. 207-211. March, 1929. (7. 93.)

A list of plants grouped under (1) in the jungle; (2) margin of jungle; (3) on Patanas; (4) rock on Patanas; (5) swamp on Patanas; (6) among the tea.

464. **Holland, T. H.** "Fodder Grass Trials on the Experiment Station, Peradeniya." *Dept. Agric. Ceylon, Bulletin* **84**, pp. 1-12, 5 plates. Feb. 1929. (7. 94.)

Notes are given on sixteen grasses, of which seven are indigenous, *Mimosa pudica* is reported a troublesome weed in plots of creeping grasses.

465. **Venkatraman, T. S. and Thomas, R.** "Studies of Sugar Roots at Different Stages of Growth." *Memoirs Dept. Agric. India, Bot. Series, Calcutta*, **16**, No. 5, pp. 145-157, 3 plates. Jan. 1929. (7. 95.)

466. **Khan, Abdur Rahman.** "Studies in Indian Oil Seeds. No. 3, *Carthamnus tinctorius* Linn." *Memoirs Dept. Agric. India, Bot. Series, Calcutta*, **18**, No. 3, pp. 81-87, 1 plate. Dec. 1929. (7. 96.)

Ten new types are described and a key to the Indian types is published.

467. **Blatter, E.** "Mosses of the Bombay Presidency, the High Wavy Mountain and Mount Abu." *Journ. Bombay Nat. Hist. Soc.* **32**, pp. 870-879. Oct. 1929. (7. 97.)

The lists are arranged alphabetically.

468. **Mayuranathan, P. V.** *The Flowering Plants of Madras City and its Immediate Neighbourhood*. Government Press, Madras. (7. 98.)

This is the *Bulletin of the Madras Government Museum, Natural History Section*, No. II, and is illustrated.

469. **Cowan, J. M.** "The Forests of Kalimpong—an Ecological Account." *Records Botanical Survey India, Calcutta*, **12**, No. 1, pp. 1-74, with coloured folding map. 1929. (7. 99.)

Kalimpong is a subdivision of the Darjeeling district situated in Northern Bengal, having an area of 412 sq. miles, of which 206 are Government Reserve Forests. These form a nearly continuous belt round the subdivision and enclose a large area of cultivated land in the centre. The country is very mountainous, the whole of the north-eastern part being over

5000 ft., and on the Rechi La near the Sikkim-Bhutan boundary the mountains reach an elevation of over 10,000 ft.

The climatic conditions depend largely upon the south-west monsoon. Most of the rain falls between June and October and the lower slopes of the hills facing the monsoon have a yearly rainfall of 200 in., while the north-west slopes have about 120 in. At lower elevations where rainfall exceeds 180 in., evergreen species predominate, but with less than 160 in. most of the trees are deciduous and shed their leaves during the hot season (April and May) when the mean maximum temperature is about 96° F. At elevations above 4000 ft. where the temperature is equable the majority of trees are evergreen.

In the absence of sufficient data regarding succession the author takes altitude as the chief factor in determining the distribution of the forest communities. These are grouped under three zones: (1) the Tropical or Lower Hill zone; (2) the Subtropical or Middle Hill zone; and (3) the Temperate or Upper Hill zone. In all the zones the climax community is forest, alpine vegetation on the Himalayas developing above 12,000 ft. The Lower Hill zone ascends from the river valleys to about 3000 ft. and occupies about 95 sq. miles. The forests are mainly deciduous, except in the districts of high rainfall where evergreen forest develops. Four plant communities, described as associations, are recognised: (1) the *Shorea-Terminalia-Garuga*; (2) the *Shorea-Stereospermum*; (3) the *Schima-Bauhinia*; and (4) the *Eugenia-Phoebe*. For each of these associations the author gives a list of species showing the percentage composition of the community. Thus, *Shorea robusta* forms 34.4 per cent. of the first, but only 13.3 per cent. of the second association. *Schima Wallichii* constitutes 18.6 per cent. of the third association. These figures which refer to dominant species are sufficient to show that the several associations comprise a considerable assemblage of species. A number of these is recognised as forming consociations or societies and these are mentioned under the name of the locally dominant species. In the Subtropical or Middle Hill zone, lying between 3000 and 6000 ft., much of the land is under cultivation. Even 50 years ago the area under forest was much greater in this zone than it is now. Man has been responsible for the disappearance of the greater part of the forests between 3000 and 6000 ft. over an area of about 188 sq. miles. This has been due mainly to a rapid increase in the agricultural population. In the Middle Hill zone four climax associations are recognised: (1) the *Castanopsis-Schima*, (2) the *Schima-Castanopsis-Phoebe*, (3) the *Engelhardtia-Castanopsis-Schima-Betula*, and (4) the *Ostodes* association. In this zone only about 30 sq. miles are under forest and the third association mentioned is the chief tree community. Its European character is rather remarkable, for, although the species are different, many European genera are represented. The Temperate or Upper Hill zone ranges from 6000 to 12,000 ft. The area under forest is about 78 sq. miles. The following communities are determined chiefly by altitude: (1) the *Machilus-Michelia* association occurring from 6000 to 7000 ft.; (2) the *Quercus* association from 7000 to 9000 ft.; (3) the *Rhododendron* association on the slopes of the higher ridges; and (4) the *Tsuga-Abies* association represented in the Kalimpong area by a few isolated groups.

The author concludes his survey by giving a short account of seral communities, dealing with the succession in river beds, burnt areas, waste lands, forest coupes and on landslips.

470. Blatter, E. "Revision of the Flora of the Bombay Presidency, Parts 8-11." *Journ. Bombay Nat. Hist. Soc.* **32**, pp. 229-243, 480-496, 753-775. 1929. **33**, pp. 12-26. March, 1930. (7. 100.)

Starting with the subfamily Pooideae the Gramineae are completed. A key to the family and an alphabetical list of genera is furnished.

## (8) TROPICAL AND NORTH AFRICA (COLLABORATOR, T. F. CHIPP)

471. Thompson, H. N. *Report Regarding the Irregularities of Rainfall in Nigeria*, pp. 16, 3 graphs. The Government Printer, Lagos. 1928. (8. 42.)

The *Report* is a special publication in which is discussed the extent of the association between a growing irregularity of rainfall and the progress of desiccation in Nigeria. The discussion centres round the theory advanced by Schonken in recent years before the South African Association for the Advancement of Science. The records available for Nigeria are admittedly too meagre to test the theory satisfactorily, but the inference is that the Nigerian records do not tend to confirm it. A plea is again advanced for the preservation of natural vegetation, for conserving the water supply of dry regions by the preservation of the natural vegetation, especially along streams and water divides, and to prevent herds and flocks invading these areas.

472. *Tsetse Research Annual Report for the year ended 31st March, 1929*, pp. 1-18. The Government Printer, Dar-es-Salaam, Tanganyika Territory. 1929. Price 2s. 6d. (8. 43.)

This is the first *Report* published by the Director of Tsetse Research. The subject is being treated as an ecological proposition. The *Report* deals with the several investigations, which have been undertaken. It is too early as yet for any definite results to be ascertained, though useful lines of research have been indicated. The studies in animal and plant ecology of the district and the influence of fire in control and combat of the fly are described.

473. *Tsetse Reclamation Annual Report for the year ended 31st March, 1929*, pp. 1-10. The Government Printer, Dar-es-Salaam, Tanganyika Territory. 1929. Price 1s. 6d. (8. 44.)

This is a progress report of the effort made to reclaim country infested with fly and to check its advances.

474. Phillips, J. F. V. "Some Important Vegetation Communities in the Central Province of Tanganyika Territory." *South Afr. Journ. Sci.* **26**, pp. 332-372. Dec. 1929. (8. 45.)

The author's object is to give a preliminary account of the principal vegetation communities within the Central Province and to suggest their successional relations. A brief description is given of the area in question, the geology, physiography, soils, and climatic conditions. It is shown that the climate is subtropical with two dry and two rainy seasons each year. The vegetation is described as coming within two formations, a term used in the sense of F. E. Clements. The formations are termed the Deciduous Scrub, on alluvial and eluvial soils below 1400 metres, and the Subtropical Evergreen Forest above 1400 metres. The open grassy "mbuga," or periodically moist alluvial sunklands, appear to provide a Grassland climax, but it is pointed out that these areas support seral communities, not climax, and are successional to woody communities at lower and higher elevations alike.

A considerable number of communities are enumerated with brief notes and lists of principal species.

The subject has been studied primarily in connection with Tsetse fly investigations.



(9) CENTRAL AND SOUTH AMERICA (COLLABORATOR, R. C. McLEAN)

475. Williams, R. O. and Cheesman, E. E. *Flora of Trinidad and Tobago*, Vol. I, Part 2, *Parietales*, *Polygalineae*, *Caryophyllineae*, *Guttiferales*, *Geraniales*, by R. O. Williams. *Malvales*, by R. O. Williams and E. E. Cheesman. Dept. of Agriculture; Trinidad and Tobago. 1929. 6s. (9. 10.)

This is the third part of this Flora to be issued, the two previous parts being Vol. I, Part 1, *Ranales*, and Vol. II, Part 1, *Rubiales*. The effects of old settlement are reflected in the large number of naturalised and introduced species included. The botanist of temperate zones cannot but be impressed by the fact that *Cruciferae* are represented by four species only (three being casuals) and *Caryophyllaceae* by one weed, while on the other hand *Malvaceae* run to nineteen genera with thirty-nine species and *Malpighiaceae* to twelve genera with thirty-two species. Local names are cited, and it is evident that when plants can be baptised "Scotch Attorney," "Jump-up-and-kiss-me" or "The Hatstand Tree," the Saxon tongue has not lost its cunning in this matter. Distribution of species in neighbouring areas is recorded.





## Supplement VIII

### BRITISH EMPIRE VEGETATION ABSTRACTS:

#### TITLES AND ABSTRACTS OF PUBLICATIONS ON THE VEGETATION AND ECOLOGY OF THE OVERSEAS EMPIRE AND ON RELATED TOPICS

##### (1) CANADA (COLLABORATOR, J. E. DANDY)

476. Adams, J. "A Bibliography of Canadian Plant Geography to the End of the Year 1920." *Trans. Roy. Can. Inst.* 16, pp. 293-355, and 17, pp. 103-145, 227-265. 1928-30. (1. 126.)

This deals not only with the Dominion of Canada but also with the adjacent territories of Alaska and Labrador, the islands of Newfoundland, St Pierre, and Miquelon, and the Arctic Islands to the north of Canada. The bibliography is divided into six sections, dealing respectively with six chronological periods: before the end of the year 1800, 1801-50, 1851-75, 1876-1900, 1901-10, and 1911-20. Under each of these sections the names of authors are arranged in alphabetical order.

477. Hitchcock, C. L. "Revision of North American Species of *Godetia*." *Bot. Gaz.* 89, pp. 321-361, Fig. 1. 1930. (1. 127.)

According to this revision only one species of *Godetia* (Onagraceae) is represented in Canada, namely *G. amoena*, of which two varieties, var. *typica* (a new name) and var. *gracilis* (a new combination based on *G. gracilis*), extend northwards from the western United States into British Columbia.

478. Faull, J. H. "Notes on Forest Diseases in Nova Scotia." *Journ. Arnold Arb.* 11, pp. 55-58. 1930. (1. 128.)

This article comprises notes on some of the forest diseases observed by the author during a pathological reconnaissance of the forests of Nova Scotia, which he carried out in July, 1929, as a preliminary to the study of the forest diseases of the province. A number of the diseases seen had not previously been reported from Nova Scotia; these new records are marked with asterisks throughout the paper.

479. Raup, H. M. "A New Species of *Salix* from the Mackenzie Basin." *Rhodora*, 32, pp. 111-112, Plate 202. 1930. (1. 129.)

A new species of willow, *Salix athabascensis*, is described and illustrated from material collected by the author in northern Alberta.

480. Bishop, H. "The Austin Collection from the Labrador Coast." *Rhodora*, 32, pp. 59-62. 1930. (1. 130.)

The author gives a brief account of a collection of plants made by him as a member of the Austin expedition to the coast of Labrador in the summer of 1928. Plants were gathered at twenty stations along the southern and central parts of the coast, from Battle Harbour in the south to Tikkoatokok Bay in the north, representing a stretch of some 400 miles. The vegetation shows, in exposed situations, the general depressed habit of the crowberry (*Empetrum nigrum*) and the bearberry (*Arctostaphylos alpina*), but becomes a low forest

of black spruce (*Picea mariana*) with a dense lichen turf, mostly of *Cladonia alpestris*, in sheltered valleys. In at least this section of the coast the flora has a conspicuous Canadian character, and its age, origin, and affinities appear to have a definite relation to the extensive glaciation in recent geological times. The potency of this factor is easy to see in the almost total absence of soil, the low rounded hills of essentially uniform height, and the countless boulders everywhere to be seen. The rarity of certain species would seem to indicate the disappearance of the older arctic flora of the region, and the dominance of others points to the invasion of a more southern flora. Thus the spread northwards of Canadian types at the close of Pleistocene times appears to be the main clue to the origin of the Labrador flora.

At the end of the paper are appended notes on some of the more interesting plants collected on the expedition.

481. Allen, A. F. "Some *Cladoniae* from the Valley of the Cap Chat River and Vicinity, Gaspé Peninsula, Quebec." *Rhodora*, 32, pp. 91-94, Plate 199. 1930. (1. 131.)

This comprises a list of lichens of the genus *Cladonia* collected by the author during July and August, 1928, in the valley of the Cap Chat River and on Mt Logan, a near-by peak of the Shickshock Mts, in Matane County, Quebec, near the north shore of the Gaspé Peninsula. One species (*C. invisa*) is described as new by C. A. Robbins, who also proposes the new combination *C. conista* (based on *Cenomyce fimbriata* var. *conista*) for another. Notes are added on a few of the more interesting forms.

482. Kennedy, R. B. "Some Additions to the Newfoundland Flora." *Rhodora*, 32, pp. 3-4. 1930. (1. 132.)

Six plants not previously reported from Newfoundland were collected by the author while botanising in the south-west of the island from mid-June to mid-September, 1929. They are *Hydrocotyle americana*, *Anemone riparia*, *Impatiens pallida*, *Potamogeton subnitens*, *Lotus corniculatus*, and *Crepis biennis*.

483. Raup, H. M. "The Pollinization of *Habenaria obtusata*." *Rhodora*, 32, pp. 88-89, Fig. 1. 1930. (1. 133.)

*Habenaria obtusata* is a common plant of the Canadian forest from Newfoundland to Alaska. In the Athabaska-Great Slave Lake region of north-western Canada it is not only extremely abundant, but also by far the most common of all the orchids growing there. On several occasions mosquitoes have been found carrying the pollinia of this orchid, the sticky pads of the pollinia being fastened to the heads of the insects near the base of the mouth-parts. It is possible that the great abundance of the orchid is due to an efficient pollinisation carried on by the myriads of mosquitoes which inhabit the woods. The flowers produce sufficient scent and nectar to attract such sugar-loving insects.

484. Fernald, M. L. "Contributions from the Gray Herbarium of Harvard University—No. LXXXVII. II. *Carex macrocephala* and *C. anthericoides*." *Rhodora*, 32, pp. 9-11. 1930. (1. 134.)

The North American sedge which was formerly identified with the north-eastern Asiatic *Carex macrocephala*, and which occurs on the Pacific coast from southern Alaska to Oregon, is a distinct species whose correct name is *C. anthericoides*. True *C. macrocephala* is now establishing itself on the Atlantic coast of North America, in New Jersey.

485. Fernald, M. L. "Contributions from the Gray Herbarium of Harvard University—No. LXXXVII. IV. The Complex *Bromus ciliatus*." *Rhodora*, **32**, pp. 63-71, Plate 196. 1930. (1. 135.)

*Bromus Dudleyi*, described as a new species by Fernald, ranges from Newfoundland to British Columbia and southwards into the United States. In habitat it shows a marked preference for (though not restriction to) limy or neutral bogs and wet thickets, being specially characteristic of the calcareous regions of Newfoundland, the Mingan Islands, the Gaspé Peninsula, etc. It is closely allied to *B. ciliatus*, and has been confused with that species, which is the commonest *Bromus* of thickets and borders of woods in eastern Canada and the north-eastern United States. *B. ciliatus* itself is subdivided by Fernald into two varieties, both of which are Canadian plants. To the typical variety, which is generally more northern in distribution and shows a strong subalpine tendency, he gives the new name *B. ciliatus* var. *genuinus*. The other and less boreal variety is diagnosed as new under the name *B. ciliatus* var. *intonsus*.

486. Fernald, M. L. "Contributions from the Gray Herbarium of Harvard University—No. LXXXVII. V. Some Varieties of the Amphigean Species of *Osmunda*." *Rhodora*, **32**, pp. 71-76. 1930. (1. 136.)

In this paper three species of *Osmunda* are discussed. The North American representative of *O. regalis* is maintained as *O. regalis* var. *spectabilis*; it occurs from Newfoundland to the Saskatchewan and southwards in the eastern United States. *O. Claytoniana*, in its typical variety, ranges from Newfoundland to Lake Winnipeg and to the eastern United States. *O. cinnamomea* exists in three geographical varieties, of which only one, var. *typica* (a new name), is found in Canada, where it extends from Newfoundland to Ontario.

487. Fernald, M. L. "Contributions from the Gray Herbarium of Harvard University—No. LXXXVII. VI. *Potamogeton alpinus* and *P. microstachys*." *Rhodora*, **32**, pp. 76-83, Plate 197. 1930. (1. 137.)

The American plants which have been referred to *Potamogeton alpinus* (sometimes as *P. alpinus* proles *microstachys*) are here regarded as constituting a distinct species for which Wolfgang's name *P. microstachys* is taken up. The species falls into two varieties, of which var. *typicus* (a new name) is widespread in Canada, whilst var. *subellipticus* (diagnosed as new) occurs from Newfoundland to British Columbia.

488. Fernald, M. L. "Contributions from the Gray Herbarium of Harvard University—No. LXXXVII. VII. The Identities of *Juncus canadensis* and of *J. brevicaudatus*." *Rhodora*, **32**, pp. 83-88, Plate 198. 1930. (1. 138.)

In this paper the correct application of the names *Juncus canadensis* and *J. brevicaudatus* is discussed at length, the conclusions reached being at variance with the views expressed by K. K. Mackenzie in a previous article (see Abstract 391).

489. Stebbins, G. L., Jr. "Contributions from the Gray Herbarium of Harvard University—No. LXXXVII. III. A Revision of Some North American Species of *Calamagrostis*." *Rhodora*, **32**, pp. 35-57, Plate 195. 1930. (1. 139.)

This revision deals with the North American species of *Calamagrostis* sect. *Calamagris* and sect. *Dejeuxia* subsect. *Orthoatherae*. A key to the species is given, followed by an enumeration of them and their varieties. Eight of the species are represented in Canada,

these being *C. canadensis* (six varieties), *C. Scribneri* (var. *imberbis*), *C. cinnoides*, *C. expansa* (vars. *typica*, *robusta*, and *brevior*), *C. crassiglumis*, *C. labradorica*, *C. neglecta* (type and vars. *borealis* and *micrantha*), and *C. lapponica* (var. *brevipilis*). A number of the varietal names are new.

490. Fernald, M. L. "A New Willow from the Côte Nord, Quebec." *Rhodora*, 32, pp. 112-113, Plate 203. 1930. (1. 140.)

*Salix simulans* is described and illustrated as a new species from specimens collected at Betchewun, Saguenay County, Quebec.

491. Bill, J. P. "*Carex Knieskernii* Dewey." *Rhodora*, 32, pp. 162-166. 1930. (1. 141.)

*Carex Knieskernii* is a rare sedge of Canada and the United States. It has been considered to be of hybrid origin, but Bill favours the view that the plant is a valid species.

492. Eames, E. H. "*Cubelium concolor*." *Rhodora*, 32, pp. 140-142. 1930. (1. 142.)

The nearly or quite glabrous phase of *Cubelium concolor* (Violaceae) is proposed as a new form, f. *subglabrum*. It extends from the eastern United States into southern Ontario.

493. Blake, S. F. "The Names *Aster ericoides* and *A. multiflorus*." *Rhodora*, 32, pp. 136-140. 1930. (1. 143.)

In this paper Linnaeus's name *Aster ericoides*, which has been misapplied by practically all authors since W. Aiton, is taken up for the North American species usually known as *A. multiflorus*. The species which has generally passed for *A. ericoides* should be called *A. pilosus*. New combinations are made for varieties and forms of these two species, and a new variety (*A. pilosus* var. *demotus*) is proposed for a common form which occurs in Ontario and the eastern United States.

494. Ostenfeld, C. H. and Petersen, H. E. "On a New Plasmodiophoracea Found in Canada." *Zeitschr. für Bot.* 23, pp. 13-18, Figs. 1-6. 1930. (1. 144.)

A Canadian Plasmodiophoracea collected by Ostenfeld in August, 1924, is proposed as the type of a new genus (*Membranosorus*) under the name *M. Heterantherae*. The fungus was found infesting the roots of *Heteranthera dubia* (Pontederiaceae) growing in Lake of the Woods, western Ontario.

495. Rydberg, P. A. "Notes on Fabaceae—XII." *Bull. Torr. Bot. Club*, 56, pp. 539-554. 1930. (1. 145.)

Rydberg here deals with North American species of the genus *Astragalus* (in a restricted sense). Several of the species mentioned occur in Canada.

(2) SOUTH AFRICA (COLLABORATOR, A. W. EXELL)

496. Levyns, Margaret R. "Floral Evolution and Geographical Distribution in *Lobostemon*." *S. Afr. Journ. Sci.* 27, pp. 317-322, 1 Diagram. 1930. (2. 80.)

Evolutionary series in the genus *Lobostemon* and the geographical distribution of the species are discussed and evidence is given that hybridisation is a factor of importance.



497. Verwoerd, L. and Dippenaar, B. J. "Descriptions of some new Species of South African Fungi and of Species not previously recorded from South Africa." *S. Afr. Journ. Sci.* **27**, pp. 326-330. 1930. (2. 81.)

New species of *Cercospora*, *Septoria*, *Cladosporium*, *Diplodia*, *Pestalotia*, and *Coccophora* are described.

498. Marloth, R. "A Revision of the Group *Virosae* of the Genus *Euphorbia* as far as represented in South Africa." *S. Afr. Journ. Sci.* **27**, pp. 331-340, Plates IV-VI. 1930. (2. 82.)

Four new species of *Euphorbia* are described and figured and a key is given to the South African species of the group *Virosae*.

499. Phillips, J. F. V. "Fire: its influence on Biotic Communities and Physical Factors in South and East Africa." *S. Afr. Journ. Sci.* **27**, pp. 352-367. 1930. (2. 83.)

An outline is given of the more important changes in the vegetation following firing, in (i) climax grassland, (ii) tree-and-grass savanna developing to either deciduous or evergreen scrub climaxes, (iii) Macchia or "Fijnbosch," (iv) subtropical and tropical evergreen forest. Vast stretches of South and East Africa have their vegetation kept in an "open" or non-climax condition by annual or periodic fires. In the tree-and-grass savannas fire has played a considerable part in the development of certain growth forms in plants and profoundly affects the behaviour of the animals associated with the vegetation. Firing also brings about far-reaching changes in the physical, chemical and biological conditions in soils. The conclusion is reached that *controlled* firing is a useful and often necessary agent in veld management and tsetse-fly control, but it is urged that generalisations regarding the influences of firing should be made only after the local circumstances have been examined.

500. Mogg, A. O. D. "An Aut-ecological Note on the Poisonous 'Gifblaar' (*Dichapetalum cymosum* (Hook.) Engl.)." *S. Afr. Journ. Sci.* **27**, pp. 368-375, Plate VII and 1 Chart. 1930. (2. 84.)

*Dichapetalum cymosum* (Hook.) Engl. is found to produce young shoots twice in the season probably owing to the evenness of the soil temperature during the period Aug.-Nov. and again in March. These young shoots are very toxic.

501. Cuthbert, J. B. "Some Notes on the Physiology of *Teloschistes flavicans*." *Trans. Roy. Soc. S. Afr.* **19**, pp. 27-44, Plate III and Text-figs 1-6. 1930. (2. 85.)

In the Cape Peninsula *Teloschistes flavicans* is almost invariably supported by *Asparagus capensis* L.; its distribution is limited and erratic. The water relations, presence of parietin and "weathering" are discussed.

502. Rennie, J. V. L. "Note on Fossil Leaves from the Banke Clays." *Trans. Roy. Soc. S. Afr.* **19**, pp. 251-253, Text-figs A-J. 1931. (2. 86.)

Some seventy fragments of dicotyledonous leaves referable to at least twelve species have been found in the Banke clays. The material is very incomplete but gives a glimpse of a past flora of a type distinct from that of the modern flora of Little Namaqualand and which could only have flourished when the climate of that region was considerably more humid than it is at present.



503. Compton, R. H. "The Flora of the Whitehill District." *Trans. Roy. Soc. S. Afr.* 19, pp. 269-329. 1931. (2. 87.)

This is a systematic list of the species of a small area surrounding and including the Karoo Garden at Whitehill; the total area covered being about 40 square miles. There are two main topographical formations. Firstly the Karoo, an undulating area of Dwyka and Ecca rocks, of a general altitude of about 3000 ft. This area is generally rocky, and in some parts is thickly strewn with stones: the soil is generally shallow, but areas of deeper soil occur. The vegetation varies greatly according to circumstances. Secondly the Witteberg range of mountains which provide a sharply contrasting formation with a vegetation totally distinct from that of the Karoo.

New species are described in the genera *Bulbine*, *Massonia*, *Leucospermum*, *Thesium*, *Aizoon*, *Heliophila*, *Crassula*, *Aspalathus*, *Pelargonium*, *Zygophyllum*, *Agathosma*, *Diosma*, *Polygala*, *Hermannia*, *Arthrosolea*, *Erica*, *Salaxis*, *Scyphogyne*, *Microlophos*, *Sutera*, *Ostia*, *Aster*, *Felicia*, *Pteronia*, *Helichrysum*, *Helipterum*, *Rosenia*, *Phymaspermum*, *Euryops*, *Othonna*, *Osteospermum*, *Tripteris*, and *Ursinia*. The new genera *Cromidon* and *Globulariopsis* are described in the Selaginaceae, and *Alatoseta* and *Thodaya* in the Compositae.

504. Tischer, A. "*Corpuscularia perdiantha* Tisch. spec. nov." *Monatsschr. Deutsch. Kakteen-Gesell.* 2, pp. 20-21. 1930. (2. 88.)

505. Schwantes, G. "Neue Mesembriaceen. V." *Monatsschr. Deutsch. Kakteen-Gesell.* 2, pp. 21-22. 1930. (2. 89.)

Descriptions of new species of *Agnirictus* and *Conophytum*.

506. Schwantes, G. "Neue Mesembriaceen. VI." *Monatsschr. Deutsch. Kakteen-Gesell.* 2, pp. 64-69, 2 Photographs. 1930. (2. 90.)

Descriptions of four new species of *Ruschia*.

507. Schwantes, G. "*Pleiospilus Nelii* Schwant. sp. nov." *Monatsschr. Deutsch. Kakteen-Gesell.* 2, pp. 146-147, 3 Photographs. 1930. (2. 91.)

508. Dinter, K. "Die Sukkulanten der Buchberge." *Monatsschr. Deutsch. Kakteen-Gesell.* 2, pp. 215-220. 1930. (2. 92.)

This is an account of the succulents found on an expedition to the Buchu Mts in South-west Africa.

509. "Notes from the British Museum Herbarium." *Journ. of Bot.* 68, pp. 49 and 246. 1930. (2. 93.)

Descriptions of the new species *Gazania venusta* Taylor and *Heliophila Salteri* Exell.

510. "Novitates Africanæ." *Journ. of Bot.* 68, pp. 75-79 and 102-107. 1930. (2. 94.)

Descriptions of new species in the genera *Oxalis*, *Aspalathus*, *Cyphia*, *Erica*, *Salvia* and *Hebea* by L. Bolus, in the genera *Crassula* and *Huernia* by N. Pillans, in the genus *Conophytum* by Lavis, in the genus *Bobartia* by Gillett, and a description by R. H. Compton of the new genus *Urgineopsis* in the Liliaceae.

511. Salter, T. M. and Exell, A. W. "Some New Species of *Oxalis* from South Africa." *Journ. of Bot.* 68, pp. 143-146. 1930. (2. 95.)

Seven new species of *Oxalis* are described from Cape Province.

512. Smith, C. A. "*Nuxia* and *Lachnopylis* in Africa." *Bull. Misc. Inf. Kew*, pp. 10-32, Text-figs 1-2. 1930. (2. 96.)

South African species formerly referred to *Nuxia* are transferred to the genus *Lachnopylis* and a key is given to the species occurring in South Africa.

513. Smith, C. A. "*Scilla lanceaefolia* of the Flora Capensis." *Bull. Misc. Inf. Kew*, pp. 241-252. 1930. (2. 97.)

New names are published for a number of *Scilla* spp. from South Africa.

514. Marquand, C. V. B. "A New Species of *Exorhodothea* from South Africa." *Bull. Misc. Inf. Kew*, pp. 237-239, 1 Text-fig. 1930. (2. 98.)

515. Schonland, S. "The South African Species of *Rhus* L." *Bothalia*, 3, pp. 3-115 with numerous Text-figs. 1930. (2. 99.)

This important genus with numerous species in South Africa is dealt with in detail as regards classification, phylogeny, morphology, habit and geographical distribution.

516. Forbes, Helena M. L. "The Genus *Psoralea* Linn." *Bothalia*, 3, pp. 116-136. 1930. (2. 100.)

A key to the South African species of *Psoralea* is given together with descriptions of all the species and their geographical distribution.

517. Marloth, R. "Notes on *Aloe spicata* Linn. fil." *Bothalia*, 3, pp. 142-146, 2 Photographs. 1930. (2. 101.)

518. Stent, S. M. "South African Gramineae. Some New Species of *Digitaria*." *Bothalia*, 3, pp. 147-156. 1930. (2. 102.)

(3) AUSTRALIA AND TASMANIA (COLLABORATOR, V. S. SUMMERHAYES)

519. Williamson, H. B. "Notes on the Victorian Species of *Cassia*." *Victorian Naturalist, Melbourne*, 46, pp. 175-8. Jan. 8th, 1930. (3. 37.)

Six species are admitted as possibly Victorian. A key to these is given, with descriptions and notes on each species.

520. Summerhayes, V. S. "A Revision of the Australian Species of *Frankenia*." *Journ. Linnean Society, London, Botany*, 48, pp. 337-387, Plates 16-18, 7 Text-figs. April 24th, 1930. (3. 38.)

Forty-five species including the introduced *F. pulverulenta* are enumerated and described. A synopsis of the series of Australian species and a key to the species are provided.

521. Rupp, H. M. R. *Guide to the Orchids of New South Wales*. Pp. viii + 152, 84 Photographs, 8 Text-figs. Angus and Robertson Ltd, 89, Castlereagh Street, Sydney. 1930. (3. 39.)

Popular descriptions of all the species are given, with partial synopses to some of the larger genera. Many notes on habitat and other biological details. Habit photographs are supplied of many of the species.

522. Patton, R. T. "The Factors controlling the Distribution of Trees in Victoria." *Proc. Roy. Soc. Victoria, Melbourne*, 42, pp. 154-210, Plates 15-20, 4 Text-figures, 2 Maps. March 13th, 1930. (3. 40.)

The factors are classified into three main categories: (A) Climatic, (B) Geological,

(C) Biotic.

(A) The climatic factors are discussed under the following headings: (a) Rainfall, (b) Evaporation, (c) Temperature, (d) Ocean Currents, (e) Wind.

(a) Rainfall. In the greater part of Victoria the rainfall is fairly evenly distributed throughout the year, but is slightly greater in the winter months. The rainfall is considered from three points of view: (1) Average Annual Precipitation, (2) Monthly Distribution, (3) Reliability. For the purposes of tree distribution the State can be divided into four areas with over 40 in., 30-40 in., 15-30 in., and under 15 in. annual rainfall respectively. Most of the forests occur in the first two divisions. In the areas with over 40 in. rainfall the monthly distribution is so even as not to interfere with the development of climax temperate rain forest, but in the other areas the low summer rainfall is often a limiting factor. Under (3), reliability, the importance of drought years to tree species is pointed out, the limit of endurance being reached in many places in the dry years 1923 and 1927. The effect is not very noticeable in the areas with rainfall over 40 in. The possibility of the occurrence of several consecutive years of low rainfall in a district has not always been considered in the interpretation of meteorological data.

(b) Evaporation. The relative humidity of the air bears no definite relationship to transpiration taking place, whereas evaporation can be used as a reliable index of the transpiration. The evaporation occurring in an area can be calculated approximately from the average temperature and relative humidity. How often the evaporation exceeds the rainfall is of great importance to tree species.

(c) Temperature. The distribution of *Eucalyptus rostrata* and *E. ovata* is controlled by temperature, the boundary line between them being somewhere between the 55° and 60° isotherms, *E. rostrata* occurring in the hotter regions and *E. ovata* in the cooler.

(d) Ocean Currents. The presence of a number of tropical trees and lianes in East Gippsland is due to the warm current southwards along the coast of New South Wales.

(e) Wind. It is suggested that certain eucalypts are gradually invading Victoria from South Australia as a result of the prevailing south-west and north-west winds distributing the seeds eastwards.

(B) Geological factors are of more importance in the distribution of plants than is usually admitted. Palaeozoic sedimentary rocks support poor forests, whereas igneous rocks of the same age bear the finest forests in Victoria. In the Cainozoic regions the sedimentary rocks bear forests in the areas with higher rainfall, but the basalt is almost treeless.

(a) Soil. The physical characteristics are very important, most eucalypts only occurring on light soils, while the basalt, which normally forms heavy soils, rarely bears forest. The distribution of *Eucalyptus viminalis* in its relation to soil types is thoroughly discussed. On the whole grasslands are found on heavy soils and forests on light soils, this being independent of the climate. As the mountain ranges are composed of acid igneous rocks whereas the alkaline basalt always forms plains no real comparison of the effect of these two different chemical types can be made. The effect of water content and the nature of the subsoil is also discussed. The presence of an impervious clay layer not far below the surface is inimical to tree development.

(b) Physiography. This is treated under the headings Elevation, Contour and Slope. In the Australian Alps *Eucalyptus coriacea* is the only species reaching to the timber line at 5500 ft. (1650 m.). *E. gigantea*, however, although only found up to 4500 ft. (1350 m.),

does not pass below 3000 ft. (900 m.) and is therefore a subalpine species. On the whole, areas with sharp contours bear forest, while plains, at whatever altitude, are covered with grassland. The different vegetation of north and south slopes is also dealt with shortly.

(C) Biotic. Observations show that fire can have played little part in determining the distribution of tree species in Victoria in the past. Very old trees of fire-sensitive types have been recorded from many places. Since settlement by white men fires have caused great changes in the forests, producing finally communities of *Pteridium*.

(8) TROPICAL AND NORTH AFRICA (COLLABORATOR, T. F. CHIPP)

523. Theriot, I. "Mousses du Congo Belge et du Liberia récoltées par H. D. Linder." *La Revue Bryologique*, 57 Année, t. 3, fasc. 1-2: pp. 30-50, 14 Figs. 1930. (8. 46.)

An enumeration of Congo and Liberian mosses collected by the Expedition of the Harvard Institute of Tropical Biology and Medicine, 1926-27.

524. ANNUAL AGRICULTURAL REPORT FOR 1929, *Somaliland Agricultural and Geological Department*. The Crown Agents for the Colonies, 4 Millbank, London, S.W. 1. pp. 30. May, 1930. (8. 47.)

In a section devoted to "Soils" the Director of Agriculture remarks that some twenty years ago the whole of the neighbourhood of the Military Headquarters at Burao was heavily wooded with large thorn-tree Acacias, and, though, for military reasons, most of the large trees and brushwood within the necessary distance from the headquarters were cut down to provide a field of fire, outside the ring so formed both trees and brushwood still covered the ground. During the last few years a gradual dying-off of this vegetation has become very noticeable, large areas are already merely dusty sand-plain, and it is clear that unless steps are taken to arrest it and to replant the bare ground, much larger areas will soon become completely denuded.

Further, it has been found that in places in Burao difficulty is experienced in growing either trees, crops or flowers of any kind, though the soil, which is a sandy alluvium, cannot be regarded as unfavourable. One of the reasons suggested is that, with the cutting down of the large trees and the continual breaking up of the bare surface, the soil regularly exposed to the Kharif and other winds is carried off as clouds of dust which, partly checked by the remaining vegetation, settles round it and ultimately chokes it.

525. NYASALAND PROTECTORATE. *Annual Report of the Forestry Department for the Year ended 31st December, 1929*. The Government Printer, Zomba, pp. 14. 1930. (8. 48.)

There are a few references to the occurrence of the principal timber trees. The Report is chiefly administrative.

526. Chipp, T. F. "Forests and Plants of the Anglo-Egyptian Sudan." *Geog. Journ.* Royal Geographical Society, Kensington Gore, London, S.W. 7, 75, No. 2, pp. 123-143, 8 Plates, 1 Fig., 3 Maps. February, 1930. (8. 49.)

The country is not a natural entity and the author first describes the botanical region of which it forms part. To this region he gives the name of the West African Botanical Region, and in it includes all tropical Africa encircling the Gulf of Guinea as far as the Atlas Mountains in the north, and Abyssinia and the Rift Valley in the east. The belts of vegetation which stretch in great transcontinental bands from west to east are shown to be

controlled by the climate based on the Gulf of Guinea monsoon. The development of the vegetation diminishes correspondingly as the distance from the coast increases. Four main climatic types of vegetation are recognised. The closed forest nearest the sea, then the grass woodland, in which the proportion and density of the woodland varies; two sub-types are described, the *Azelia-Butyrospermum-Lophira* and the Combretaceous. This is followed by the thorn scrub (*Acacia-Balanites-Capparis*), and finally there is the Saharan desert vegetation (*Acacia-Panicum*), in which occur areas devoid of all life.

Other types are the edaphic, which embrace the vegetation of the great lakes, and the mangroves along the sea front; the physiographic, which is represented by the montane vegetation; whilst the result of the activities of man are shown in the biotic climax.

The main types of vegetation which pass into the Anglo-Egyptian Sudan are then discussed in detail and their principal constituents noted. Edaphic climaxes are illustrated by reference to the *Acacia* forests along the Nile, and to the great Sudd swamps.

A physiographic climax is illustrated from the vegetation, now recorded for the first time, from the Imatong Mountains in Southern Mongalla. The author briefly discusses the general distribution of the montane vegetation of Africa.

527. **Bannerman, D. A.** *The Birds of Tropical West Africa.* The Crown Agents for the Colonies, 4 Millbank, Westminster, S.W. 1, pp. lxxv + 376, 10 full page plates and maps in colour, 119 Text-figs. 1930. Price 22s. 6d. (8. 50.)

Although primarily an enumeration, with descriptions, of the birds of Tropical West Africa, the author has devoted some considerable space to the vegetation of the area in a section devoted to the relationship of the vegetation belts to the distribution of bird life in Tropical Africa. The area in the north is bounded by the river Senegal, on the east by longitude 20° E., on the south by the river Congo, whilst in the west the Cape Verde and Gulf of Guinea islands are included.

The map in colours showing the vegetation belts has been specially prepared for this work and forms the subject of a note by Dr T. F. Chipp. The main object of the book is to enable the observer in the field to identify the birds, and in this connection valuable "field identification" notes have been compiled from the records of travellers. To aid the novice without any technical knowledge of ornithology, an illustrated key has been specially prepared which enables the principles of classification to be mastered comparatively easily. A bibliography; a record of the ornithological history of the British Colonies, a glossary of technical terms, and a comprehensive index are also included. By its wide scope this book not only becomes the standard work on the subject for West Tropical Africa, but also a reference work for all countries which are visited by the birds described.

The author's efforts to produce a work of first-class importance have been ably seconded by the publishers, who have produced a volume worthy of the author's treatment.

A preface by the Secretary of State for the Colonies acknowledges the assistance rendered by the British West African Governments and the British Museum (Natural History).

528. *Annual Report of the Forest Department for the year ended December 31st, 1929, Uganda Protectorate.* The Government Printer, Entebbe, pp. 15. 1930. Price Sh. 1/50. (8. 51.)

The section of the Report headed "Formation and Regeneration of Forests" states that no satisfactory method of procuring natural regeneration in indigenous forests has so far been found in Uganda. When conditions favourable for germination and growth of the valuable timber species which it is desirable to regenerate are produced these conditions



are also favourable for worthless species and weeds which grow very much more rapidly and swamp the desirable regeneration.

Species of Eucalyptus have been used in planting swamps with the idea of draining. The experiment is in too early a stage to form any opinion as to its success.

529. Chipp, T. F. "The Vegetation of the Central Sahara." *Geogr. Journ.* 76, No. 2, pp. 126-137, 2 Maps, 8 Plates. August, 1930. Price 2s. (8. 52.)

During a recent journey across the central Sahara, an opportunity was taken to record the vegetation types existing south of the Mediterranean flora on the slopes of the Atlas Mountains and north of the flora of the French Sudan in the vicinity of the Niger, a country botanically unknown. The route followed was a general direction due south of Algiers to the Ahaggar massif.

The African flora as represented by an edaphic type, with the Acacias and *Panicum turgidum*, was found to occur at the southern escarpment of the Tadmait Plateau, and in all the dry river systems and drainage plains southwards.

The ephemeral, or "acheb," vegetation, the most northerly type controlled from the Gulf of Guinea monsoon, was noted.

References are given to the vegetation of the oases, and to the cultivation methods generally practised in the country.

The results of the observation on the vegetation are discussed in relation to the general distribution of the belts of vegetation for north tropical Africa.

530. Wells, C. "The Colour of Ruwenzori." *Geogr. Journ.* 76, pp. 110-125, 7 Plates and 1 Text-fig. 1930. (8. 53.)

A description of a rather laborious method of colour photography by matching with standard colours is given, followed by a general account of the Massee Ruwenzori Expedition. The plates give very good impressions of the vegetation, and include excellent pictures of giant *Senecios* and *Lobelias*. The wretched living conditions on Ruwenzori are stressed, with the object of enabling future expeditions to be more suitably equipped. The observations made are quite general, and it is to be hoped that more exact details will appear elsewhere.

531. Sykes, R. A. "Some Notes on the Benin Forests of Southern Nigeria." *Empire Forestry Journ.* 9, pp. 101-106, 1 Fig. 1930. (8. 54.)

A short description of the geology, topography and rainfall variation of the area is followed by a more detailed account of the vegetation, which is divided into (a) Closed Forest, (b) Open Forest, and (c) Grassland. The first of these forms the main subject of the paper and is divided into six subsections, each of which is discussed in turn from the point of view of dominant forest trees. Some interesting notes with regard to a few species are included. Clearings made by farmers at various times provide interesting seral communities in various stages of development. Changes in the relative frequency of the dominants are very noticeable in travelling inland, though floristic change is slight.

532. Swynnerton, C. F. M. *Annual Report on Experimental Reclamation, Department of Tsetse Research, Tanganyika Territory, for the year ended March 31st, 1930.* Crown Agents for the Colonies, London, pp. 1-24, 1 Map, 3 Plates. 1930. Price 1s. (8. 55.)

An account is given of the second programme of work carried out at Shinyanga, devoted chiefly to the exclusion of fly from areas to which organised grass-burning is inapplicable. Experimental methods are the making of palisades to exclude animal visitors and the provision of clearings and semi-natural thickets too wide for the fly to cross unaided.



The analysis of losses from the live-post palisade gives much information on the relative susceptibility of native trees to termites and other less important causes of loss. Resistance to fire, changed environment and clearing operations is noted.

- 533.** *Nigerian Forestry Department, Bulletin No. 1. Record of Forest Research in 1928.* Government Printing Office, Lagos. Pp. 42, 10 tables and charts. 1930. Price 5s. (8. 56.)

The *Bulletin* is a summary of the first year's work of the Research Officers of the Forestry Department. The greater part is taken up with an account of the research operations at the Forest Experiment Stations at Sapoba and Olokemeji. Useful information is given of the sylvicultural characteristics and records of the periodicity of many of the forest trees. A third section contains an account of the anti-erosion operations at Udi.

- 534.** **Prat, H.** "Influence des Brouillards sur la Végétation du Djebel Murdjadjo." *Bull. Trimestr. de la Société de Géographie et d'Archéologie d'Oran.* (Noticed in *Geogr. Journ.* Oct. 1930, p. 363.) (8. 57.)

Investigations on the vegetation confined to the upper part of the scarps in the Oran district, showed that its presence is due to the mists which develop in the evening after a hot day. The mist is prevented from enveloping the bottom by the hot air currents which dissolve it.

- 535.** **Barnes, A.** "The flora of the equatorial highlands of Africa." *Journ. Roy. Hort. Soc. London*, **55**, Part 2, pp. 266-270. September, 1930. (8. 58.)

A popular account of the author's lecture on his travels in the Central African highlands and the Atlantic islands.

- 536.** **Dalziel, J. M.** "Cameroon Mountain." *Scot. Geogr. Mag.* **46**, pp. 257-274, Figs 1-6. Sept. 15th, 1930. (8. 59.)

A general account of the geography and geology of the mountain is followed by a more detailed account of its known volcanic activity, with special reference to the eruptions of 1907 and 1922. After briefly discussing rainfall and other water supplies, Dr Dalziel proceeds with the main object of the paper, which is an account of the vegetation and phytogeography of the mountain. The close similarity of the flora to that of the high mountains of East Africa is strongly stressed, the absence of arborescent *Senecio* spp., and such sharply differentiated zones as the Bamboo Forest Zone of East Africa being noted. Resemblance to the South African flora, as exemplified by the presence of *Helichrysum* spp., is stated to be purely superficial. Affinity with the European flora is noted, and a short list of familiar genera common to both areas is given. The paper concludes with a useful bibliography.

- 537.** **Phillips, J. F. V.** "The application of ecological research methods to the Tsetse (*Glossina* spp.) problem in Tanganyika Territory: a preliminary account." *Ecology*, **11**, pp. 713-733. Oct. 1930. (8. 60.)

This paper was read before the British Association for the Advancement of Science at Johannesburg in July, 1929, and is an account of the work and methods employed by the Department of Tsetse Research, Tanganyika Territory. A brief history of the work is given: it was begun single-handed by the present director of the department, Mr C. F. M. Swynnerton, in 1921. The department was formed in 1925, but the preliminary work occupied three years, and it was not until 1928 that the department was reorganised to attack the Tsetse problem on an ecological basis. Short paragraphs on "concept" and past work are followed by the more detailed account of the work, divided into the following sections:

(1) Reconnaissance; (2) Autecology of Tsetse; (3) Synecology of Tsetse: Non-physical Aggregations; (4) Synecology of Tsetse: Interrelation of the Biome, the Physical Environment, and Tsetse; (5) Interrelations of Tsetse and the Vertebrate Fauna; (6) Biological Control. It is hoped (Conclusion) that the methods outlined will lead eventually to complete control of Tsetse and the attendant sleeping sickness or trypanosomiasis. The Summary is followed by a note on Dr Townsend's paper "The Tsetse Problem" (*S. Afr. Journ. Nat. Hist.* 4, No. 1, pp. 36-45; No. 2, pp. 139-145, 1923) and a list of literature cited in the text.

538. Hagerup, O. "Étude des Types Biologiques de Raunkiaer dans la flore autour de Tombouctou." *Det Kgl. Danske Videnskabernes Selskab, Biologiske Meddelelser*, 9, 4, pp. 1-116, 5 Figs, 5 Plates. København. 1930. (8. 61.)

The author recounts an intensive investigation into the flora around Timbuctu during his three months' residence. The great influence of the wind in dispersing fruits and seeds, so that their distribution is almost uniform, is discussed. The intimate relationship of the rainy period and germination is pointed out, and the rapidity with which some plants pass through the whole of their living phase is instanced. The time required, however, varies according to environmental conditions. The different classes of Raunkiaer's divisions are discussed in the light of the examples studied. A systematic enumeration of the species collected is given, with notes on their geographic distribution. Very interesting observations on the physiology of the plants are offered and indications given as to the type of plant most likely to succeed on introduction. The Chamaephytes represent the dominant biologic type, but the greater part of the biologic types tend to become Therophytes; certain species appear under two different biologic types. In discussing the spectra it is shown that the Chamaephytes have a percentage of 36 compared with 9 of the normal spectrum; the Chamaephytes are better able to live through all the seasons. If a species ventures too far northwards it perishes in the great desert, whose southern limit constitutes the characteristic line of demarcation in plant distribution. The statistical determination of biologic types by Raunkiaer's system affords the best method of ascertaining the geographical limitations of the different kinds of plant life.

539. Hagerup, O. "Über die Bedeutung der Schirmform der Krone von *Acacia Seyal* Del." *Dansk Botanisk Arkiv*, 6, Nr. 4, pp. 1-19, 5 Figs, 1 Plate. København. 1930. (8. 62.)

*Acacia Seyal* is a tree with an umbrella-shaped crown of the thorn bush (Savanna) country of the Sudan. The physiology and assimilatory organs are described and it is stated that the twigs are the chief assimilation organs of the tree. These are extended so as to make the most use of the sunlight, and when this cannot be effected, as with the twigs in the under part of the crown, they die off, and so the umbrella shape is obtained. The thorns, when dead, are white and reflect the light, throwing it on to the least illuminated sides of the twigs. The leaves, which are developed only in the summer season, are accessory organs of assimilation. The structure of the organs discussed is described in detail.

540. Strong, Richard P. *The African Republic of Liberia, and the Belgian Congo. The Harvard African Expedition*, 1926-27, Vol. I, pp. xxvii + 1-568, 9 Maps, Plates nos. 1-443, 2 Text-figs. Vol. II, pp. ix + 569-1064, Plates nos. 444-476, Text-figs nos. 3-28. 1930. Price \$15 the set. (8. 63.)

The expedition travelled in Liberia, then traversed the Belgian Congo along the Congo River and the Lualaba, thence across the continent through Uganda and Kenya to the east coast. The greater part of the report is devoted to sociology, pathology, and zoology. The

preliminary chapters deal with the geography and climate of Liberia so far as known, the authors confining themselves to the politically contained Liberia, and not treating it as part of the biological region of West Africa. Chapter XII contains one page on the geology, and twenty-five devoted to a general discussion of the vegetation encountered by the expedition from the point of view of its comparison with other tropical vegetation with which the members of the party were familiar in tropical America. Chapter XXXII (fifty-seven pages), entitled "Botanical Report of Liberia," is a descriptive narrative of the tour with lists of the plants noticed en route. No complete enumeration of the plants collected is given, and no informative account of the vegetation of this little-known area. The chief contribution is that the closed forest is found generally within some thirty miles of the coast line, and extends over the whole country, only in the extreme north and in the vicinity of the Mandingo Plateau is there anything resembling "park-like" country. The species cited are normal for this type of vegetation. The full value of the large number of illustrations and of the maps is diminished by the reduction, so that detail is lost and place names are very difficult to read.

- 541.** "Le Déboisement du Sénégal. Actes et Comptes Rendus de l'Association Colonies—Sciences." *Revue de Botanique Appliquée*. Pp. 225–230. Nov. 1930. (8. 64.)

A comparison of early accounts of the vegetation of certain parts of Senegal with those of recent visitors, especially that of M. Auguste Chevalier. The rapid destruction of the vegetation is recorded, and the reason attributed to the extension of ground-nut cultivation, to pasturage, and to the firewood requirements of an increasing population. The subsequent article (pp. 230–233) discusses this question in connection with French Tropical Africa generally.

- 542. Armand, Annet.** "Reconnaissance dans le nord Mauritanien." *La Géographie*, **54**, Nos. 1–2, pp. 13–23, 2 Maps, 3 Photographs, 2 Figs. Paris, Juillet-Août, 1930. (8. 65.)

A general description is given of the country situated about 19° N. and 12° W. No direct reference is made to the vegetation, but the illustrations show the country to be typically Saharian—sandy plains and rocky mountains.

- 543. Prince Sixte de Bourbon.** "De Djibouti à Khartoum par Addis Abeba, le Beni Changoul et le Soudan." *La Géographie*, **54**, Nos. 1–2, pp. 1–12, 2 Maps. Paris, Juillet-Août, 1930. (8. 66.)

From Addis Abbaba a six-wheeled automobile was used for the 250 km. westwards to Billo, a journey which took three days. Thence the journey was by small mules which covered some 30 km. a day with a load of 45 kg. During the last stages native porters were employed. The Anglo-Egyptian Sudan was entered at Kurmuk. Brief references are made to the vegetation, more especially cultivations and shade trees such as Eucalyptus and giant "Sycamores." The destruction due to firing the dry vegetation in the Beni Changoul is described.

- 544. Leakey, L. S. B.** "East Africa Past and Present." *Geogr. Journ.* **76**, No. 6, pp. 494–498. The Royal Geographical Society, London, S.W. 7. December, 1930. Price 2s. (8. 67.)

The author discusses the recent physiographic history of Tropical East Africa during the establishment of man in the country. The possibilities of the populations and domestic animals which can be carried are considered in relation to the vegetation of the present day, and the variations in the types of vegetation which may be effected by alteration in the water supply are dealt with.

545. **Nicholson, J. W.** "Forests and Rainfall." *Empire Forestry Journal*, 9, No. 2, pp. 204-212. The Empire Forestry Association, 22 Grosvenor Gardens, London, S.W. 1. 1930. Price 7s. 6d. (8. 68.)

The evidence that forests do influence rainfall, so far as observations in East Africa have been carried out by the author, is more positive than negative in character. The author discusses the subject at length and weighs the evidence as to what influence forests exert over the different kinds of precipitation, basing his arguments on his experience in East Africa.

546. **Topham, P.** "Man and The Forest in Northern Nyasaland." *Empire Forestry Journal*, 9, No. 2, pp. 213-220. The Empire Forestry Association, 22 Grosvenor Gardens, London, S.W. 1. 1930. Price 7s. 6d. (8. 69.)

The area described is the part of Nyasaland west of the Lake. The main vegetational types are divided into a "deciduous" type which is nearly leafless for some months of the year, and an "evergreen" in which the leafless period is very short. Both types contain all physiognomic forms of vegetation. The practice of shifting cultivation and its influence on the succession of forest types are discussed.

547. **Kennedy, James D.** "Taungya Method of Regeneration in Nigeria." *Empire Forestry Journal*, 9, No. 2, pp. 221-225. The Empire Forestry Association, 22 Grosvenor Gardens, London, S.W. 1. 1930. Price 7s. 6d. (8. 70.)

The possibilities of developing this system in the Sapoba district and the effect of the system on the vegetation are discussed.

548. **Mildbraed, Dr J.** "Sample Plot Surveys in the Cameroons Rain-Forest." *Empire Forestry Journal*, 9, No. 2, pp. 242-266. Empire Forestry Association, 22 Grosvenor Gardens, London, S.W. 1. 1930. Price 7s. 6d. (8. 71.)

This is one of the first records of sample plot surveys in the West African equatorial forest. The plots were each 1 hectare in area. As the survey was required for utilisation purposes only stems of 30 cm. diameter and upward were reckoned. The system employed is detailed, and records of several plots given, with the author's comments on each plot. The gaps in the age classes is a most striking feature, and also the influence of the habitat factors on the composition of the plots. No attention was apparently paid to the possibility of discontinuous germination. A systematically arranged check-list of all the plants collected in the Likomba forest is given. The translation from the German is by H. M. Heyder.